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General Introduction to Southwest Nova Scotia Fisheries Ecology Program (FEP): 1982–89[1]

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(JA411)

The full complexity of a marine ecosystem is not easily appreciated by rigorously investigating a single aspect (e.g. trophic level) of that system while treating other aspects either superficially or not at all. On the other hand, cross-evaluation and synthesis of the results from several different studies, from a multidisciplinary perspective, often leads to new insights into the interactions among the various trophic levels of the system and between the system and the physical environment. In this vein, scientists from various government laboratories and universities in Atlantic Canada set out in 1982 to study the ecology of the commercially important gadoid fisheries on the southwestern Scotian Shelf, with a specific focus on the Browns Bank haddock stock. The ultimate goal of the project, known as the Fisheries Ecology Program (FEP), was to provide sound advice for management of the fisheries through increased knowledge of how the system works. Projects within the FEP addressed a wide range of topics from physical oceanography to planktonic and benthic productivity, factors affecting ichthyoplankton condition and dispersal, reproductive and feeding biology of fish, fish stock distribution and dynamics, and fleet fishing patterns and fishery management. Initial planning lead to a series of cooperative field and laboratory studies over 3 yr (1983–85) during which contacts among investigators were maintained both informally and through regular communications such as a newsletter and an annual review of progress.

The preliminary results of this venture have been published as a block of six papers in a regular issue of this journal (Volume 46, No. 4, April 1989; FEP No. 1–6, see below). Primarily, these results highlight work within a single discipline, since scientific ''cross-fertilization'' usually requires some initial growth as an ''individual.'' The present volume contains more of the ''individual'' contributions (FEP No. 7–18), but also offers a pair of ''synthesis'' papers (FEP No. 19, No. 20) which attempt to draw together individual results in order to explore possible relationships between events in the early life history and year-class strength of a fishery (Campana et al. FEP No. 19) or between physical and biological factors affecting the initiation of the spring bloom off southwest Nova Scotia (Perry et al. FEP No. 20).

With regard to the physical environment, strong annual cycles in water mass properties are found to be controlled by both air–sea interaction and alongshore advection by the Nova Scotian Current (Smith FEP No. 7). On the other hand, interannual variability in both physical properties and plankton is related primarily to anomalies in alongshore wind stress that are associated with variations in atmospheric pressure over the North Atlantic (Smith FEP No. 7; Koslow et al. FEP No. 9). A model for mixed-layer development during the 1983–85 winter and spring seasons is reasonably successful in predicting an early and sustained development of the spring bloom in 1985, based on the concept of a critical depth for initiation of the bloom (Perry et al. FEP No. 20).

Careful studies of ichthyoplankton have demonstrated several important facts about the early life history of gadoid species in relation to the physical environment. For instance, despite differences in timing, Browns Bank is the primary spawning site for both Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (Hurley and Campana FEP No. 14). Temperature does not appear to affect the time of peak spawning for haddock (as it does for cod), but interannual temperature differences can cause variations in total duration of egg stages from 10–30 d (Page and Frank FEP No. 11). Stratification also strongly affects the vertical distribution of eggs and larvae in the water column such that buoyant, newly-spawned eggs are concentrated near the surface, but in latter stages tend to sink to mid-depth near a position of neutral buoyancy where their degree of aggregation is controlled by the strength of the stratification (Page et al. FEP No. 10; Frank et al. FEP No. 12). The vertical distribution of larvae tends to parallel that of the late stage eggs, so that in low density nearshore waters, they are likely to encounter the bottom where survival rates are typically low. Such a mechanism could prevent colonization of the nearshore zones and thereby define the distributional limits of the early life history stages (Frank et al. FEP No. 12). Water column stability also has a profound effect on growth characteristics of haddock larvae as indicated by the above (below) average growth rates observed in stratified (well-mixed) areas (Frank and McRuer FEP No. 16). Growth rates of postlarval cod also showed important regional differences with nearshore rates inferior to these on Browns Bank (Suthers et al. FEP No. 15). This study demonstrates a close coupling of the dispersal and growth processes which is considered to be important in shaping reproductive success of marine fish populations.

The dispersal of haddock larvae from their Browns Bank spawning site was examined through age-structured analysis of the sampled spatial distributions and found to be bimodal: part of the larval population was retained on the Bank, while the remainder was advected to the inshore region (Campana et al. FEP No. 13). Although such a phenomenon is presumably related to the competition between the retentive capabilities of the Browns Bank gyre and dispersive tendencies of tidal and wind-driven currents, a model for particle dispersion in the surface layer was incapable of reproducing the observed behaviour of either the larvae or of drogued drifters (Page and Smith FEP No. 8). This negative result compromised, to some extent, the attempt to identify which early life history stage is most influential in the determination of year-class strength, since egg and larval mortalities could not be consistently linked to advection from the spawning sight as determined by the model. However, the abundance and mortality of the juvenile stage were found to be useful indices of year-class strength (Campana et al. FEP No. 19).

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[1] This is part of a series of papers devoted to the Fisheries Ecology Program.

With regard to the distributions of adult fish, it was found that demersal fish assemblages on the Scotian Shelf are strongly related to depth, but that there are no clear assemblage boundaries. As expected, assemblages on the western Scotian Shelf and in the mouth of the Bay of Fundy are dominated by haddock (Mahon and Smith FEP No. 17). In addition, studies of the reproductive biology of the western Scotian Shelf haddock have revealed details of the location, timing, and physical environment of spawning, size at maturity, and changes in gonad size during maturation and fecundity (Waiwood FEP No. 18).

Though much has been accomplished thus far, many FEP studies are presently ongoing, particularly with regard to the adult stocks. Future publications in this area will include (1) a comparison of haddock food and feeding patterns between offshore banks and nearshore zone at the mouth of the Bay of Fundy, (2) an analysis of the seasonal distributions and growth patterns of haddock based on FEP trawl surveys, and (3) a determination of the utility of stratification intensity as a proxy for larval condition and possibly year-class strength of haddock. In addition, continued work on the particle dispersion model will address several notable weaknesses in an attempt to improve the comparison with observations. With increased confidence in model predictions, further attempts to interpret interannual differences in abundance and mortality of early life stages might prove more fruitful.

Finally, with regard to improving advice to fisheries managers and the fishing industry, FEP has made some contributions to resolving practical concerns such as stock definition, recruitment forecasting, environmental issues, and fishery regulation for haddock and cod in NAFO Subarea 4X. Concurrent egg and larval surveys on Browns and Georges Banks (Hurley and Campana FEP No. 14) revealed differences in timing of haddock spawning and limited exchange of ichthyoplankton between the two banks, which supports the existence of reproductively isolated haddock stocks. This information will be used in connection with the restriction of trawler fishing activity in spawning areas. Restrictions on trawlers might also be considered for juvenile nursery areas identified on Browns Bank and along the inshore 100 m isobath (Suthers and Frank FEP No. 4) because of the potentially significant by-catch of juvenile fish.

The heavy commercial exploitation of haddock and cod stocks on Browns Bank leads to reduced life spans and limited spawning opportunities. Thus, the yield of these fisheries depends on the strength of the incoming year classes. One FEP result suggests that year-class strength is established in the late larval/early juvenile stages (Campana et al. FEP No. 19), so that comprehensive juvenile surveys may provide a lead time of almost 2 yr for recruitment estimation. In addition, the information about the reproductive biology of southwest Nova Scotia haddock (Waiwood FEP No. 18) has been incorporated into the analysis of stock and recruitment of haddock in NAFO subarea 4X. Though small, these FEP findings represent significant advancements in knowledge of southwest Nova Scotia fisheries and our ability to manage them.

References

FEP Contribution No.

1. Smith, P. C. 1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.
2. McLaren, I. A., M. J. Tremblay, C. J. Corkett, and J. C. Roff. 1989. Copepod production on the Scotian Shelf based on life-history analyses and laboratory rearings. Can. J. Fish. Aquat. Sci. 46: 560–583.
3. Wildish, D. J., A. J. Wilson, and B. Frost. 1989. Benthic macrofaunal production on Browns Bank, Northwest Atlantic. Can. J. Fish. Aquat. Sci. 46: 584–590.
4. Suthers, I. M., and K. T. Frank. 1989. Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in southwestern Nova Scotia determined with two different gear types. Can. J. Fish. Aquat. Sci. 46: 591–602.
5. Campana, S. E., and P. C. F. Hurley. 1989. An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 46: 603–613.
6. Boudreau, P. R., and L. M. Dickie. 1989. Biological model of fisheries production based on physiological and ecological scalings of body size. Can. J. Fish. Aquat. Sci. 46: 614–623.
7. Smith, P. C. 1989. Seasonal and interannual variability of current, temperature, and salinity off southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 4–20.
8. Page, F. H., and P. C. Smith. 1989. Particle drift in the surface layer off southwest Nova Scotia: description and evaluation of a model. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 21–43.
9. Koslow, J. A., R. I. Perry, P. C. F. Hurley, and R. O. Fournier. 1989. Structure and interannual variability of the plankton and its environment off southwest Nova Scotia in late spring and early summer. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 44–54.
10. Page, F. H., K. T. Frank, and K. R. Thompson. 1989. Stage dependent verticle distribution of haddock (*Melanogrammus aeglefinus*) eggs in a stratified water column: observations and model. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 55–67.
11. Page, F. H., and K. T. Frank. 1989. Spawning time and egg stage duration in Northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 68–81.
12. Frank, K. T., F. H. Page, and J. K. McRuer. 1989. Hydrographic effects on the vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae on the southwestern Scotian Shelf. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 82–92.
13. Campana, S. E., S. J. Smith, and P. C. F. Hurley. 1989. A drift-retention dichotomy for larval haddock (*Melanogrammus aeglefinus*) spawned on Browns Bank. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 93–102.
14. Hurley, P. C. F., and S. E. Campana. 1989. Distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in the waters off southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 103–112.
15. Suthers, I. M., K. T. Frank, and S. E. Campana. 1989. Spacial comparison of recent growth in postlarval Atlantic cod (*Gadus morhua*) off southwestern Nova Scotia: inferior growth in a presumed nursery area. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 113–124.
16. Frank, K. T., and J. K. McRuer. 1989. Nutritional status of field-collected haddock (*Melanogrammus aeglefinus*) larvae from southwestern Nova Scotia: an assessment based on morphometric and vertical distribution data. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 125–133.
17. Mahon, R., and R. W. Smith. 1989. Demersal fish assemblages on the Scotian Shelf Northwest Atlantic: spatial distribution and persistence. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 134–152.
18. Waiwood, K. G., and M. -I. Buzeta. 1989. Reproductive biology of southwest Scotian Shelf haddock (*Melanogrammus aeglefinus*). Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 153–170.
19. Campana, S. E., K. T. Frank, P. C. F. Hurley, P. A. Koeller, F. H. Page, and P. C. Smith. 1989. Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 171–182.
20. Perry, R. I., P. C. F. Hurley, P. C. Smith, J. A. Koslow, and R. O. Fournier. 1989. Modelling the initiation of spring phytoplankton blooms: a synthesis of physical and biological interannual variability off southwest Nova Scotia, 1983–85. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 183–199.

Seasonal and Interannual Variability of Current, Temperature and Salinity off Southwest Nova Scotia[1]

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Smith, P. C. 1989. Seasonal and interannual variability of current, temperature, and salinity off southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46 (Suppl.1): 4–20.

Strong annual signals are found in temperature, salinity, and current measurements at two sites off Cape Sable, Nova Scotia. Differences in means and annual cycles indicate that the along-isobath current is not controlled by wind stress at these time scales. The phase of the primary peak of freshwater runoff into the Gulf of St. Lawrence (RIVSUM) is consistent with the advection of a salinity minimum to Cape Sable at an average speed of $6\ \mathrm{km \cdot d^{-1}}$, but the secondary peak is not observed and may be masked by the seasonal inflow of slope water into the Gulf of Maine via Northeast Channel. A diffusive model, forced by air–sea interaction, provides a reasonable fit to the annual temperature cycles with vertical diffusivities of $15–50 \times 10^{-4}\ \mathrm{m^2 \cdot s^{-1}}$. Correlations between residual longshore wind stress and along-isobath current, deep salinity, and temperature are consistent with wind-driven upwelling. Furthermore, warm-core rings in the slope water sometimes enhance onshore heat and salt fluxes to create positive temperature and salinity anomalies off Cape Sable, especially in late summer. February ocean temperature anomalies to 50 m are related to winter-average cross-shore wind (and related heat flux residuals), but do not persist on seasonal time scales.

De forts signaux annuels sont observés dans les mesures de température, de salinité et de courant de deux sites situés au large du Cap Sable en Nouvelle-Écosse. Les différences dans les cycles moyens et annuels révèlent que le courant longent l'isobathe n'est pas régi par la tension du vent à ces échelles chronologiques. La phase de la première pointe de l'entrée des eaux douces dans le golfe du Saint-Laurent (RIVSUM) concorde avec l'advection d'un minimum de salinité au Cap Sable à une vitesse moyenne de $6\ \mathrm{km \cdot d^{-1}}$, mais la deuxième pointe n'est pas observée et pourrait être masquée par l'apport saisonnier des eaux de ruissellement dans le golfe du Maine, via le chenal du nord-est. Un modèle de diffusion, forcé par une interaction air-mer, fournit un ajustement raisonnable aux cycles de température annuels compte tenu de coefficients de diffusion verticale de $15–50 \times 10^{-4}\ \mathrm{m^2 \cdot s^{-1}}$. Les corrélations observées entre la tension du vent résiduel le long des rives et le courant longeant l'isobathe, la salinité en profondeur et la température concordent avec la remontée des eaux amorcée par le vent. En outre, les courants chauds qui se trouvent dans les eaux de la pente continentale augmentent parfois les flux de chaleur et de sel sur le rivage et créent une température positive et des anomalies de salinité au large du Cap Sable, notamment à la fin de l'été. Des anomalies dans la température de l'océan observées en février jusqu'à 50 m sont reliées aux vents latéraux riverains moyens d'hiver (et au reste de flux de chaleur), mais ne correspondent pas à la durée des échelles chronologiques saisonnières.

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The waters off southwest Nova Scotia exhibit a rich spectrum of variability (spatial and temporal) which has been attributed to (1) the advection of temperature and salinity anomalies from the east by the Nova Scotian Current, (2) tidally-induced mean circulation and mixing, (3) meteorological forcing, and (4) proximity to Northeast Channel, the primary conduit for slope water to enter the Gulf of Maine. Bigelow (1927) was one of the first to recognize that the Nova Scotian Current carries low salinity water past Cape Sable in the late winter/early spring period and thereby makes a significant contribution to the water mass budget of the Gulf of Maine (Hopkins and Garfield 1979). Later, Sutcliffe et al. (1976) used correlation studies of hydrographic properties and river runoff into the St. Lawrence Estuary to trace the advection of temperature anomalies through the Gulf of St. Lawrence, along the Scotian Shelf and into the Gulf of Maine. More recently, Koslow et al. (1986) examined the influence of St. Lawrence River runoff on sea surface temperature and salinity using a multiple regression analysis which accounts for meteorological forcing that is, in turn, strongly correlated with precipitation and hence runoff. On a seasonal basis, they found that the advective (i.e. lagged) effect of runoff cannot be traced past the eastern half of the Scotian Shelf for temperature and past Cape Sable for salinity. They also found, however, that Boston Lightship summer salinities are most highly-correlated with eastward geostrophic wind during the previous spring and suggested that local runoff and/or slope water intrusions in the Gulf of Maine may play an important role in this correlation.

Measurements by Ramp et al. (1985) have demonstrated that the deep inflow of slope water through Northeast Channel to the Gulf of Maine undergoes a seasonal variation, with a maximum in late summer (August) and a minimum in spring (April). In winter, the inflow consists of intermittent "bursts" of axial current, with periods of 4 to 20 d, that are strongly correlated with longshore and cross-shore wind components and with the subsurface pressure field in the Gulf. The relationship between

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[1] Fisheries Ecology Program Contribution Number: 7.

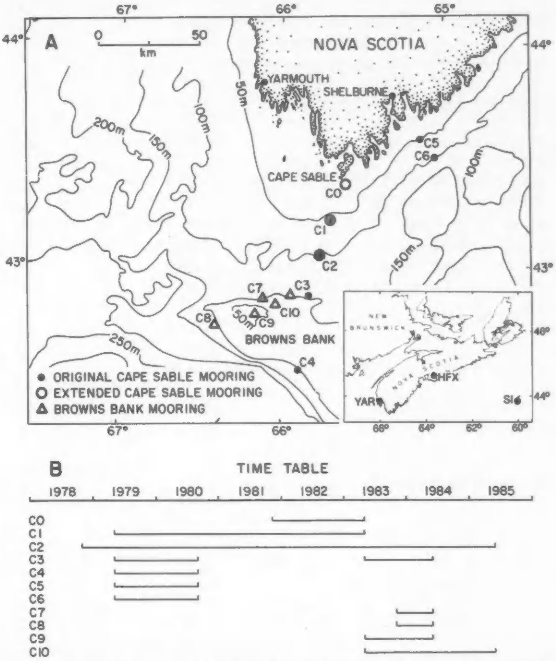

FIG. 1. Mooring array (*a*) and time table (*b*) for the oceanographic measurements off Cape Sable, Nova Scotia. The long-term observations for the present study are from sites C1 and C2 on the 60 and 110-m isobaths, respectively. The inset shows the locations of AES atmospheric measurements at Yarmouth (YAR), Halifax (HFX), and Sable Island (SI).

pressure, longshore wind, and axial current is consistent with Ekman dynamics, such that the longshore wind sets down sea level at the coast and drives a deep inflow to balance the offshore Ekman flux at the surface. In summer, a stronger, steadier slope water inflow increases the deep temperatures and salinities in the outer Gulf (Mountain and Jessen 1987) and may advect to the inner basins as part of the vernal circulation field (Brooks 1985). Ramp et al. (1985) estimate the annual mean inflow below 75 m at $2.6 \pm 0.6 \times 10^5$ $m^3 \cdot s^{-1}$, with a summer mean of 3.5×10^5 $m^3 \cdot s^{-1}$, which are consistent with water mass budgets for the region (e.g. Mountain and Jessen 1987).

The influence of Gulf Stream warm-core rings on the slope water intrusion process and interior circulation of the Gulf of Maine is not clear. Brooks (1987) documents two cases (June 1984, 1986) in which rings situated in the slope water at the mouth of Northeast Channel were associated with the presence of exceptionally warm, saline intrusions. Ramp et al. (1985), on the other hand, found that the presence of a ring on the continental slope directly off the Channel mouth produced "no noticeable effect on the currents and temperatures" within the Channel. The properties of the inflow have been characterized as either of two types of slope water found off the Scotian Shelf (Warm Slope Water (WSW) or Labrador Slope Water (LSW) (Gatien 1976)) or as modified ring water (Brooks 1987). Variations in the inflow rate and water type have a profound effect on the heat, salt, and energy budgets for the Gulf.

In 1978, a series of moored oceanographic mesurements was initiated off Cape Sable, Nova Scotia (Fig. 1), to aid in an investigation of the dynamics of the Nova Scotia Current, the tidally-induced residual circulation and the low-frequency variability associated with meteorological forcing. Using observations from 1978–80, Smith (1983) identified strong seasonal cycles in the current and water mass properties. The annual mean volumetric transport past Cape Sable was estimated at 1.4×10^5 $m^3 \cdot s^{-1}$ with a seasonal cycle of roughly the same magnitude such that the net flow into the Gulf of Maine was twice the mean in winter and nearly zero in summer. Furthermore, a clockwise gyre was found on the western cap of Browns Bank, so that the net along-isobath transport was concentrated near the coast, i.e. within the 100-m isobath. Smith also used a simple diagnostic model to suggest that the dynamics of the mean circulation are controlled by wind, a longshore pressure gradient, and horizontal gradients in the density field maintained by tidal mixing (Garrett et al. 1978; Loder and Greenberg 1986). More recently, Wright et al. (1986) have demonstrated that the results of a steady-state, wind-driven barotropic model are consistent with the observed mid-depth current response off Cape Sable, and Tee et al. (1988) have shown that monthly and fortnightly modulations of the observed currents are tidally-induced.

From 1980–83, two of the original Cape Sable moorings (C1, C2) and a new one on the 30-m isobath (CO; see Fig. 1) were

TABLE 1. Significant mean and seasonal cycles at C2.

		Mean	Annual		Semiannual		
Variable (units)	n	a_1	$A_1(\pm\Delta_1)^*$	$\phi_1(\pm\delta_1)^*$	$A_2(\pm\Delta_2)^*$	$\phi_2(\pm\delta_2)^*$	σ_R*
U2(15)($cm \cdot s^{-1}$)	63	2.77	1.66(±1.34)	11.6(±1.6)	—**	—	3.77
U2(50)($cm \cdot s^{-1}$)	59	3.23	0.95(±0.90)	9.2(±1.8)	—	—	2.39
U2(100)($cm \cdot s^{-1}$)	76	−1.23	1.75(±0.60)	1.3(±0.7)	0.77(±0.61)	11.0(±1.5)	1.86
V2(15)($cm \cdot s^{-1}$)	63	−4.31	5.62(±1.74)	7.9(±0.6)	—	—	4.86
V2(50)($cm \cdot s^{-1}$)	59	−6.58	3.93(±1.06)	7.7(±0.5)	—	—	2.84
V2(100)($cm \cdot s^{-1}$)	76	0.66	1.18(±0.62)	7.8(±1.0)	—	—	1.90
T2(15)(°C)	75	6.82	4.64(±0.25)	8.6(±0.1)	0.44(±0.25)	8.3(±1.1)	0.78
T2(50)(°C)	66	6.02	3.24(±0.31)	9.0(±0.2)	0.44(±0.31)	9.6(±1.4)	0.89
T2(100)(°C)	76	6.01	2.32(±0.36)	9.3(±0.3)	—	—	1.10
S2(15)	50	32.04	0.43(±0.18)	7.2(±0.8)	—	—	0.45
S2(50)	54	32.47	0.55(±0.13)	8.5(±0.4)	—	—	0.32
S2(100)	69	32.81	0.43(±0.11)	8.7(±0.5)	—	—	0.32

*Signals are expressed as amplitude and phase measured in months from start of the year; (Δ,δ) are estimated 95% confidence intervals (see text); σ_R = standard deviation of residual time series.

**Missing value indicates coefficient not significantly different from zero at the 95% confidence level.

TABLE 2. Significant mean and seasonal cycles at C1.

		Mean	Annual		Semiannual		
Variable (units)	n	a_1	$A_1(\pm\Delta_1)^*$	$\phi_1(\pm\delta_1)^*$	$A_2(\pm\Delta_2)^*$	$\phi_2(\pm\delta_2)^*$	σ_R^*
U1(15) ($cm\cdot s^{-1}$)	34	6.69	2.29(±1.07)	9.7(±0.9)	—**	—	2.10
U1(30)($cm\cdot s^{-1}$)	45	3.41	1.27(±0.78)	11.5(±1.2)	—	—	1.86
U1(50)($cm\cdot s^{-1}$)	47	−1.21	1.79(±0.78)	1.7(±0.8)	—	—	1.87
V1(15)($cm\cdot s^{-1}$)	34	−7.03	1.14(±1.11)	5.2(±1.9)***	1.39(±1.12)	2.6(±1.6)	2.23
V1(30)($cm\cdot s^{-1}$)	45	−4.33	2.57(±1.14)	6.1(±0.9)	1.49(±1.16)	2.3(±1.5)	2.72
V1(50)($cm\cdot s^{-1}$)	47	−1.47	0.95(±0.82)	7.9(±1.6)***	—	—	1.96
T1(15)(°C)	44	6.14	4.00(±0.35)	8.6(±0.2)	0.76(±0.34)	8.1(±0.9)	0.80
T1(30)(°C)	45	6.05	3.76(±0.37)	8.7(±0.2)	0.83(±0.37)	8.5(±0.8)	0.86
T1(50)(°C)	47	5.88	3.45(±0.34)	8.8(±0.2)	0.72(±0.33)	9.0(±0.9)	0.80
S1(15)	40	31.97	0.54(±0.21)	7.3(±0.8)	—	—	0.47
S1(30)	38	31.95	0.40(±0.19)	7.7(±0.9)	—	—	0.41
S1(50)	40	32.01	0.52(±0.20)	7.6(±0.7)	—	—	0.44

*Amplitude, phase, (Δ,δ) and σ_R as in Table 1.
**Missing value indicates coefficient not significant at 95% confidence.
***Annual cycle retained at 90% confidence level, not significant at 95%.

TABLE 3. Significant cycles in wind stress, runoff, air and sea temperatures.

		Mean	Annual		Semiannual		
Variable (units)	n	a_1	$A_1(\pm\Delta_1)^*$	$\phi_1(\pm\delta_1)^*$	$A_2(\pm\Delta_2)^*$	$\phi_2(\pm\delta_2)^*$	σ_R^*
YARTX (10^2Pa)	79	1.33	1.85(±0.43)	0.4(±0.5)	—**	—	1.37
YARTY (10^2Pa)	79	0.86	0.51(±0.37)	8.1(±1.4)	0.47(±0.37)	10.9(±1.5)	1.16
HFXTX (10^2 Pa)	79	0.48	0.81(±0.29)	0.4(±0.7)	—	—	0.90
HFXTY (10^2Pa)	79	0.43	0.43(±0.29)	10.2(±1.3)	0.37(±0.29)	0.6(±0.5)	0.90
SITX (10^2Pa)	79	1.59	2.95(±0.75)	0.2(±0.5)	—	—	2.37
SITY (10^2Pa)	79	1.97	1.33(±1.01)	11.6(±1.5)	1.83(±1.01)	0.3(±1.0)	3.16
RIVSUM (csv)***	84	1.13	0.13(±0.03)	4.7(±0.4)	0.11(±0.03)	8.6(±0.50	0.09
TAIR (°C)	79	6.77	11.21(±0.45)	7.0(±0.1)	—	—	1.41
SST(°C)	79	8.14	5.73(±0.32)	8.0(±0.1)	—	—	1.00

*Amplitude, phase, (Δ,δ), and σ_R as in Table 1.
**Missing value indicates coefficient not significant at 95% confidence level.
***csv = "centi-Sverdrups" = $10^4\cdot m^3\cdot s^{-1}$.

maintained in order to monitor inflow to the Gulf of Maine and to study the structure of the tidal boundary layer and residual current. Then in 1983, a new array of moorings was deployed on Browns Bank as part of the Fisheries Ecology Program (FEP; Smith 1989). Continuity with earlier measurements was maintained in the Browns Bank array through deployment of the C2 mooring on the inshore 110-m isobath. The result was a nearly continuous time series of moored measurements at C2 over a 6.5-yr period (November 1978 to May 1985), and an abbreviated 4-yr series (April 1979 to April 1983) at the adjacent C1 mooring on the 60-m isobath. The purposes of this work are (1) to examine the interannual variability about the annual cycles in current, temperature, and salinity over the full water column at sites C2 and C1, and (2) to attempt to relate the interannual anomalies to similar fluctuations in river runoff in the Gulf of St. Lawrence and in meteorological forcing. In spite of its importance in other regions (e.g. Myers et al. 1990), the impact of ice melt on the freshwater signal from the Gulf of St. Lawrence will be neglected, based on Bugden's (1981) estimates that its contribution is at least an order of magnitude smaller than that of runoff. The timing of the peak freshwater flux from ice melt would be somewhat earlier (March–April) than from runoff, and geographically, it would be concentrated over the Magdalen Shallows.

Moored Measurements and Related Observations

Details of the mooring configurations for the 1978–80 Cape Sable and 1983–85 Browns Bank experiments have been given elsewhere (Smith 1983, 1989), so only the salient aspects of the measurements at C1 and C2 will be discussed here. Each mooring carried at least three current meters near the surface (15 m) and bottom (10 m above) and at mid-depth. During 1980–83, six additional instruments were placed on C1 and C2 for selected periods and have been used to fill gaps in the time series at the primary depths where appropriate.

The moored instruments were mainly Aanderaa RCM-5 current meters set to sample current speed and direction, temperature, and conductivity at 30-min intervals. The estimated accuracies for deeper (mid-depth and below) measurements of the Aanderaa speed (±1.3% at speeds over 0.2 $m\cdot s^{-1}$), direction (±5°) and temperature (±0.04°C) were determined from laboratory calibrations (Smith 1989). In the surface layer (15 m), pairing of some RCM-5s with Vector Averaging Current Meters (VACMs) indicated that the Aanderaa speeds were augmented by only 0.01 $m\cdot s^{-1}$ on average, and directions differed by ±10° (Smith et al. 1984). Unfortunately, the conductivity measurements with the Aanderaa inductive cell were plagued by various problems over the course of the experiments due to design changes by the manufacturer (Boyce 1986). As a result, many of the salinity records between August 1980 and May 1984 contained variable drift errors of 0.3 to 0.6 practical salinity units (psu), representing a severe loss of data (e.g. 44% of the possible salinity data in the surface layer at C2 were lost). The remaining salinity data were accurate to ±0.10 psu based on pre- and postdeployment calibrations. Other major reasons

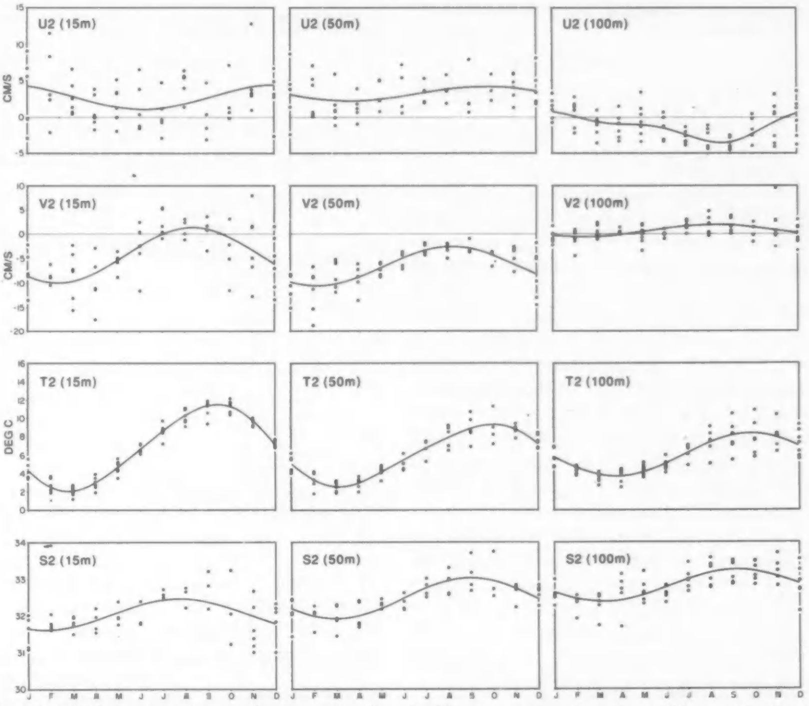

FIG. 2. Multiple regression results for mean plus significant annual and semiannual harmonics fit to monthly mean oceanographic variables at site C2. U2 = cross isobath current, V2 = along-isobath current, T2 = temperature, S2 = salinity.

for lost data include broken rotors, battery failures, and occasional damage by a fishing trawl net (Lively 1984, 1985). The temperature measurements were the most reliable, returning an average of 93% good data at the three depths on C2.

To represent atmospheric forcing, hourly wind speed and direction were collected from two AES coastal (Yarmouth and Halifax) and one offshore (Sable Island) stations for the period 1978–85. The wind speed was converted to sea surface stress using the drag law of Smith and Banke (1975) and resolved into longshore (53°T) and cross-shore (143°T) directions for the Scotian Shelf. (Wright et al. (1986) have shown that longshore wind is the dominant driving term for along-isobath flow at Cape Sable.) Similarly, the current measurements were resolved into roughly along-isobath (+V at 104°T) and cross-isobath (+U at 194°T) components and all records were low-pass filtered with a Cartwright filter (half-power point at 31 h) to remove tides and other high frequency signals.

In the following discussion, time series from a particular location will be denoted by mooring site and depth of the instrument, e.g. C2(50) represents the 50-m (mid-depth) record from C2, whereas the meteorological variables will be identified as cross-shore and longshore wind stress components at Yarmouth (YARTX,YARTY), Halifax (HFXTX,HFXTY), or Sable Island (SITX,SITY).

Methods of Analysis

To analyze seasonal cycles and interannual variations, the low-passed oceanic and wind-stress data were averaged by calender month for comparison to other monthly time series including: Halifax air temperature (TAIR); the average sea surface temperature in 43–44°N, 65–66°W, based on ships' intake temperatures (SST; Oceanographic Monthly Summary, NOAA); and RIVSUM, the combined runoff from the St. Lawrence, Ottawa, and Saguenay Rivers into the Gulf of St. Lawrence (Sutcliffe et al. 1976). Seasonal variations were then quantified, using least-squares multiple regression technique (Fofonoff and Bryden 1975), by fitting the monthly mean data for all variables (e.g. $Y_\upsilon = Y(t_\upsilon)$; t_υ = month(= 0.5 for mid-January); $\upsilon = 1,2,...N$; N = number of data points) to an estimator of the form:

$$\hat{Y}_\upsilon = \sum_{1}^{r} a_k X_{k\upsilon} = a_1 + a_2 \sin\frac{\pi t_\upsilon}{6} + a_3 \cos\frac{\pi t_\upsilon}{6} + a_4 \sin\frac{\pi t_\upsilon}{3} + \ldots$$

where

$$X_{k\upsilon} = \begin{cases} \cos(k-1)\dfrac{\pi t_\upsilon}{12}, & k \text{ odd} \\ \sin \dfrac{k\pi t_\upsilon}{12}, & k \text{ even} \end{cases}$$

includes a constant term ($k = 1$), the annual signal ($k = 2,3$) and its harmonics ($k \geq 4$). Smith (1983) has already applied this method to the first 22 mo of data from the full Cape Sable array. The regression procedure was first to fit the model function (1) with a constant plus the annual signal ($r = 3$) and test whether either coefficient (a_2 or a_3) was significantly different from zero

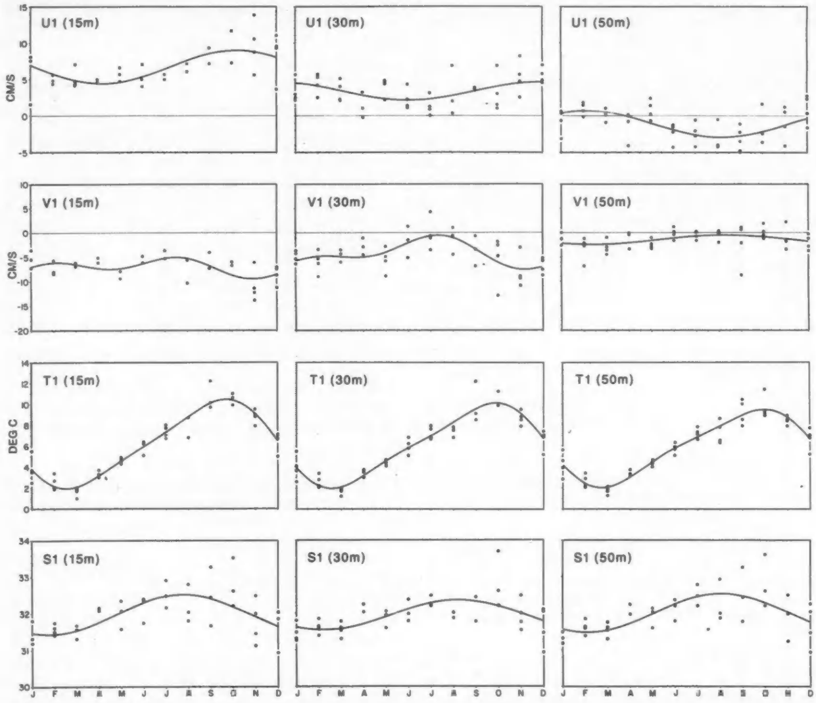

FIG. 3. Multiple regression results for mean plus significant annual and semiannual harmonics fit to monthly mean oceanographic variables at site C1. U1, V1, T1, S1 as in Fig. 2.

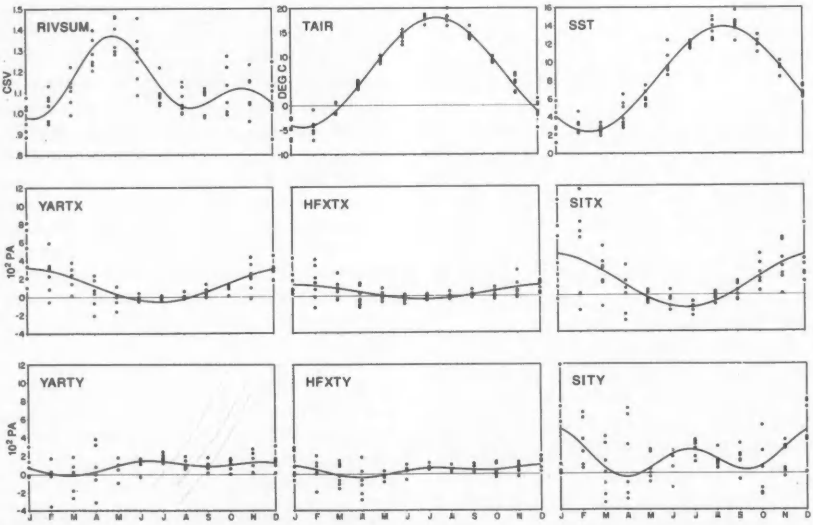

FIG. 4. Multiple regression results for mean plus significant annual and semiannual harmonics fit to monthly mean atmospheric and related oceanographic variables: freshwater runoff into the Gulf of St. Lawrence (RIVSUM); Halifax air temperature (TAIR); sea surface temperature, 43–44°N, 65–66°W (SST); cross-shore wind stress at Yarmouth (YARTX), Halifax (HFXTX), and Sable Island (SITX); longshore wind stress at Yarmouth (YARTY), Halifax (HFXTY), and Sable Island (SITY).

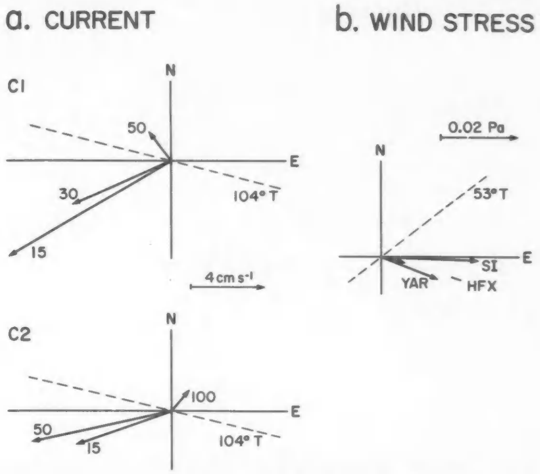

FIG. 5. Mean currents (a) at C1 and C2 and mean wind stresses (b) at Yarmouth (YAR), Halfiax (HFX), and Sable Island (SI). Dashed lines indicate along-isobath (a) and along-shore (b) directions.

at the 95% confidence level with $n-r$ degrees of freedom. If so, the procedure was repeated with $r=5$ and $r=7$ until neither of the two highest-order coefficients was significant. The series was then truncated at the last harmonic (or the constant term) which contained a significant coefficient.

This technique assumes that the monthly data are statistically independent and thereby fails to account for possible serial correlations in the residuals. However, the lagged autocorrelations of the present residuals indicate that the integral time scales for most variables are less than or of order 1 mo, suggesting that the monthly residuals are effectively independent. Furthermore, in a similar analysis of monthly mean data from Georges Bank, Butman and Beardsley (1987) demonstrated that the seasonal cycles and confidence limits produced by this method are "nearly identical" to those resulting from a more rigorous accounting for the number of independence data points using the lagged autocorrelation of the residual time series. The coefficients for significant annual cycles and first harmonics are presented here (Tables 1–3) in terms of amplitude and phase (e.g. $A_1=(a_2{}^2+a_3{}^2)^{1/2}$ and $\phi_1=\tan^{-1}(a_2/a_3)$ in months) with the associated 95% confidence limits (Δ,δ) based on those for the individual coefficients according to Butman and Beardsley (1987).

Anomaly (residual) time series were created by removing means and significant seasonal cycles (including harmonics) from the monthly mean data. To explore possible relationships between the oceanographic and other environmental variables, the lagged correlations of the anomaly data were computed for lags up to 2 yr (24 mo). The effective number of degrees of freedom for each residual time series was evaluated from the sample autocorrelation function, $\rho(m)$, as follows (Thompson et al. 1988)

$$(2)\quad \nu_{\text{eff}}=M/\sum_{-\infty}^{\infty}\rho(m)^2\cong M/\sum_{-24}^{+24}\rho(m)^2=M/\left(2\sum_{l}^{+24}\rho(m)^2-1\right),$$

where $m=0,\pm1,\pm2,\ldots$ are the lags in months and M is the number of good data. To evaluate the statistical significance of the correlations, the larger value of the summation (smaller υ_{eff}) was used as a conservative estimate. Significance levels are based on two-tailed Student t-tests with $\upsilon_{\text{eff}}-2$ degrees of freedom.

Results

Seasonal Cycles

At C2 (Fig. 2, Table 1), strong annual signals are found at all depths in the temperature, salinity and along-isobath velocity records, whereas the cross-isobath cycles are barely significant. The magnitude of the annual cycle in V is sufficient to reverse the along-isobath current in the early fall near the surface and bottom, but not at mid-depth. The phase lags of the temperature and salinity signals increase with depth, but the phase of the along-isobath current is effectively constant over the water column and generally leads that of T and S. Significant semiannual signals also exist in the temperature data at 15 and 50 m, with phases similar to those of the annual signals such that they reinforce the peak temperatures by roughly 10%. The semiannual signal in U2(100) may be spurious, considering the scatter in the data and broad confidence limits.

At C1 (Fig. 3, Table 2), the temperature and salinity cycles are similar to those at C2, except that the vertical phase differences are less pronounced. The annual signal of the along-isobath current, however, is much weaker, to the extent that only the mid-depth coefficient is marginally significant at the 95% level. Significant cycles do exist in the cross-isobath current at C1, particularly near the surface and bottom. The near-bottom currents are strongly onshore in late summer at both C1 and C2 (Fig. 3c and 2c).

Strong annual signals are also found in the cross-shore components of the wind stress at all three stations (Fig. 4, Table 3), consistent with the annual shift in the strength and location of the two principal centers of action in the atmosphere: the Azores-Bermuda High and the Icelandic Low (Blanton et al. 1985). However, the longshore stress components contain only mildly significant annual and semiannual cycles of comparable magnitude. These cycles are most pronounced in the energetic offshore records from Sable Island. (Smith (1987) has shown that at synoptic time scales (periods of 2 to 10 d), the wind stress records from Halifax and Sable Island are highly coherent in spite of an order of magnitude difference in total variance.)

Air (TAIR) and sea surface (SST) temperatures exhibit strong annual signals with TAIR having twice the amplitude and leading SST by approximately 1 mo. RIVSUM, on the other hand, has a strong semiannual as well as annual signal reflecting the secondary runoff maximum in the fall.

The mean currents (Fig. 5a) are very similar in magnitude and direction to those found by Smith (1983), but the average salinities and temperatures (except near the surface) are lower by roughly 0.2 psu and 0.4°C, respectively. The mean wind stresses computed from Yarmouth, Halifax, and Sable Island winds (Fig. 5b) are roughly eastward with positive longshore components with respect to the coastline of Nova Scotia, i.e. opposed to the along-isobath components of surface and mid-depth current.

Anomalies

The C2 anomaly time series (Fig. 6) exhibit a strong similarity over depth. This is especially true for the temperature and salinity data, whose residuals have comparable magnitude over the full water column, and for along-isobath current, whose residuals undergo a more than two-fold reduction from the sur-

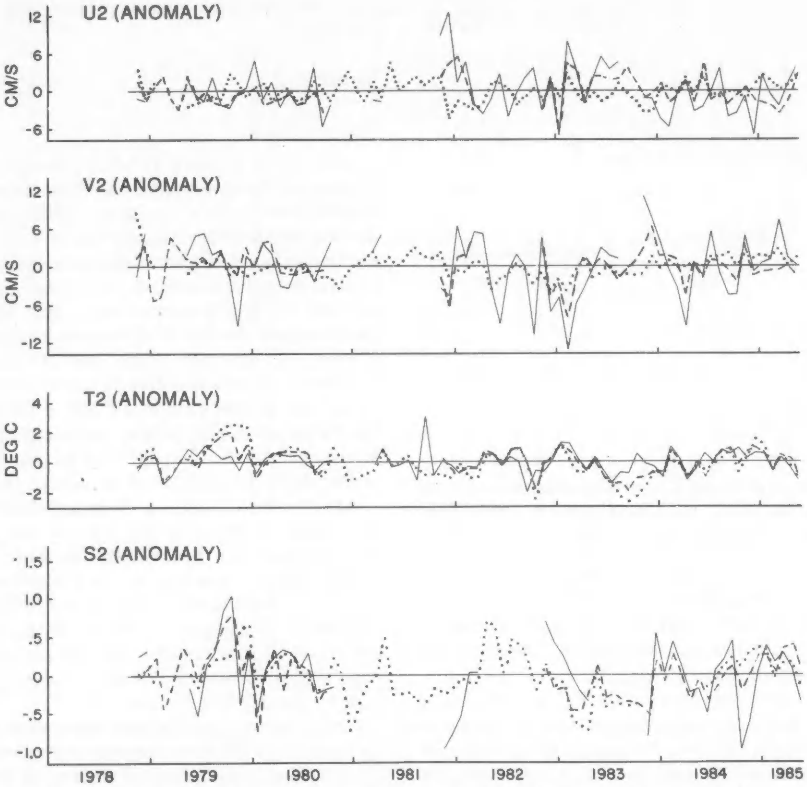

FIG. 6. C2 anomaly (residual) time series near the surface (solid), bottom (dot) and at mid-depth (dash). U2(15,50,100 m); V2(15,50,100 m); T2(15,50,100 m); S2(15,50,100 m).

face to the bottom (Table 1). Similar results obtain from the shorter records at C1 (Fig. 7), where the temperature and salinity anomalies are virtually identical as expected for a well-mixed water column.

The along-isobath current anomalies suggest that the winter of 1982/83 was a period of exceptionally strong inflow into the Gulf of Maine ($V \leqslant O$), which was followed by relatively cold, fresh conditions during the summer and early fall of 1983, especially at depth. This situation is contrasted to conditions in 1979 and early 1980 when the along-isobath current, temperature and salinity anomalies were generally positive. The longshore wind stress anomalies at Yarmouth and Sable Island (Fig. 8b) were also generally negative during the winter of 82/83, but positive or near zero during the latter half of 1979. On the other hand, the RIVSUM anomalies do not show large positive values in the year prior to the exceptionally fresh conditions in 1983, and the air temperature and SST do not reflect the relatively cold temperatures at depth in the ocean. Note, however, that the temperature anomaly at C2(15) is not as strongly negative as those at depth, suggesting some decoupling of the surface and deep layers.

Correlation Analysis

The vertical cross-correlations of the C2 velocity components are generally significant ($p \leqslant 0.05$) only between the surface and mid-depth (Table 4); temperature and salinity anomalies are well-correlated over adjacent depths. Some significant correlations are also found between the 50-m velocity components and temperature and salinity residuals. The negative correlations between U2(50) and T2(50) and S2(50) imply onshore heat and salt fluxes in the anomaly fields, whereas V2(50) and S2(50) suggest a weak eastward salt flux (or a westward flux of fresh water) on the Scotian Shelf. The temperature anomaly signal is also highly correlated ($p \leqslant 0.01$) with salinity at mid-depth and bottom, but not at the surface.

As suggested by Fig. 7, the C1 anomalies are exceptionally well-correlated in the vertical by virtue of the strong tidal mixing off Cape Sable. However, the velocity components are not well-correlated horizontally between C1 and C2, except for the near-bottom cross-isobath components (0.41; $p \leqslant 0.05$). On the other hand, temperature and salinity are well-correlated horizontally (0.57–0.88; $p \leqslant 0.01$) at 15, 50 m and along the bottom.

Some C2 current anomalies, particularly the along-isobath component, are significantly correlated with the longshore wind stress residuals from the AES stations, particularly Yarmouth (Table 5). The relationship to the cross-shore stress is weaker and confined mainly to the surface layer. Mid-depth and near-bottom salinity anomalies are also weakly-correlated with longshore stress, but no significant correlation was found with bottom or mid-depth temperature. This suggests that, in spite of the strong correlation between temperature and salinity below the surface, the forces that control the two anomalies may differ.

The Halifax air temperature anomalies (TAIR) are not significantly related to any of the oceanographic variables (Table

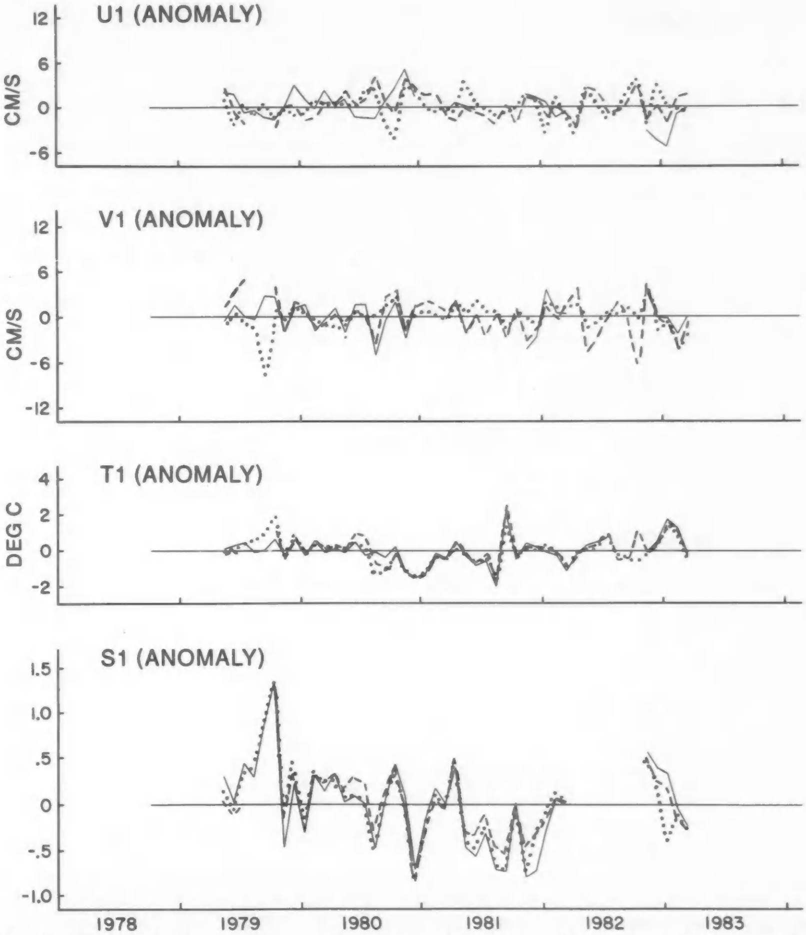

FIG. 7. C1 anomaly time series near the surface (solid), bottom (dot) and at mid-depth (dash). U1(15,30,50 m); V1(15,30,50 m); T1(15,30,50 m); S1(15,30,50 m).

5), but are strongly correlated with wind stress, particularly the cross-shore components, and to some extent with RIVSUM (Table 6). However, the spatial mean sea surface temperature (SST) is significantly correlated with T2(15) and also with T1(15) and T1(30) (not shown). This indicates that the 15-m measurements represent the temperature field over a somewhat broader scale than the immediate vicinity of the moorings. SST is also correlated with TAIR, reflecting some measure of direct atmospheric control at the surface.

Anomalies of the fresh water runoff variable (RIVSUM) showed no strong, consistent relationship to the C2 oceanographic variables at zero lag, but did indicate some significant negative correlations with the cross-isobath velocity residuals at 4–5 mo lags, and with mid-depth temperatures at 7–8 mo lags. No significant negative correlation was found between RIVSUM and C2 salinity anomalies.

Effects of Warm-Core Rings

Because of the proximity of the Cape Sable moorings to Northeast Channel, it is natural to question the extent to which the circulation and water mass properties at C1 and C2 are controlled by the strength and character of the slope water inflow to the Gulf of Maine (Brooks 1985, 1987). As noted above, the maximum salinity and temperature anomalies occurred during the fall and winter of 1979. At that time, surface frontal analysis based on satellite infrared imagery (Fig. 9) reveals that a warm-core ring (H-79) formed from a Gulf Stream meander off the mouth of Northeast Channel in early September and remained in that vicinity to the end of the year. Early in January, 1980, the ring propagated westward out of the region (not shown).

Furthermore, during a deployment cruise for the Cape Sable moorings in October, 1979, a hydrographic section from Cape Sable to Georges Bank was sampled twice in one week (Fig. 10) and indicated a dramatic change in the properties of the deep slope water inflow on the eastern side of Northeast Channel. On the first crossing (Fig. 10a,b), the maximum temperature and salinity of the slope water ($12<T<13°C$, $35.0<S<35.5$) identify it as Warm Slope Water (Gatien 1976). On the second section (Fig. 10c,d), salinities and temperatures in excess of 35.5 and 16°C, respectively, mark a ring "streamer," consisting of modified Gulf Stream water. During 15-d period bracketing the sections, the average inflow velocity at 10 m above the 110 m isobath on Browns Bank (mooring

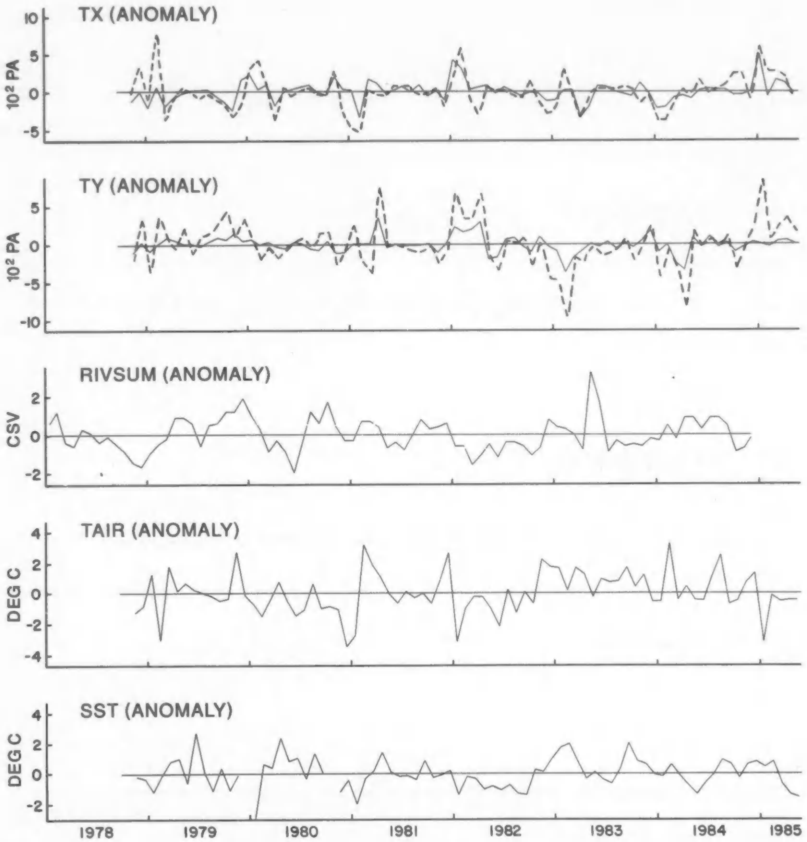

FIG. 8. Anomaly time series for atmospheric and related oceanographic variables. (TX) cross-shore wind stress at Yarmouth (solid) and Sable Island (dash); (TY) longshore wind stress at Yarmouth (solid) and Sable Island (dash); freshwater runoff (RIVSUM); Halifax air temperature (TAIR); sea surface temperature (SST).

TABLE 4. Cross-correlations of C2 anomaly data.

	U2			V2			T2			S2		
	15	50	100	15	50	100	15	50	100	15	50	100
U2(15)		.66^{d}	.04				−.28^{a}			−.35^{a}		
U2(50)			.07					−.50^{c}			−49^{b}	
U2(100)									.04			−.15
V2(15)					.76^{d}	.33^{a}	−.04			.08		
V2(50)						.34		.06			.35	
V2(100)									.10			.05
T2(15)								.67^{d}	.36^{a}	.22		
T2(50)									.88^{d}		.74^{d}	
T2(100)												.71^{d}
S2(15)											.67^{c}	.36
S2(50)												.69^{c}

[a] $p \leqslant 0.200$.
[b] $p \leqslant 0.100$.
[c] $p \leqslant 0.050$.
[d] $p \leqslant 0.010$.

TABLE 5. Cross-correlations between C2 oceanographic and environmental variables.

	U2			V2			T2			S2		
	15	50	100	15	50	100	15	50	100	15	50	100
YARTX	.23	.10	.02	$.33^{a}$	.08	−.07	.06	−.07	−.02	−.07	−.04	.12
YARTY	−.23	−.22	$-.46^{d}$	$.64^{d}$	$.56^{d}$	.18	−.05	.09	.23	.16	$.39^{a}$	$.46^{b}$
HFXTX	.19	.09	$.23^{a}$	.16	−.08	.01	−.09	−.15	.02	.05	.04	.11
HFXTY	$-.26^{a}$	−.21	$-.27^{a}$	$.59^{d}$	$.44^{c}$	.24	−.01	.14	$.28^{a}$	.18	$.42^{b}$	$.51^{c}$
SITX	$.31^{b}$	.18	.15	.06	−.12	.01	−.06	−.23	−.06	−.12	−.16	−.01
SITY	−.19	−.18	$-.26^{a}$	$.59^{d}$	$.43^{c}$	.22	−.02	.16	$.31^{a}$	.21	$.47^{b}$	$.46^{b}$
TAIR				−.13	−.11	−.03	.10	.02	−.03	−.06	−.15	−.03
SST				−.14	−.07	.07	$.36^{c}$	.05	−.06	.09	−.12	−.10
RIVSUM	.17	.06	.09	−.09	−.13	−.25	.15	.15	.23	.00	.08	.08
-3^{e}			$.26^{a}$		$-.34^{a}$							
−4	$-.34^{b}$	$-.36^{a}$						$.33^{a}$			$.38^{a}$	
−5	$-.30^{a}$						$.25^{a}$					
−6				$.27^{a}$								
−7					$.32^{a}$			$-.36^{a}$				
−8							$-.24^{a}$	$-.39^{a}$				
−9							$-.30^{b}$					

$^{a}p \leq 0.200$.
$^{b}p \leq 0.100$.
$^{c}p \leq 0.050$.
$^{d}p \leq 0.010$.
^{e}Significant cross-correlations for oceanographic variables lagged by *m* months behind RIVSUM are indicated by "−m".

TABLE 6. Cross-correlations between environmental variables.

	TAIR	SST
RIVSUM	$.26^{a}$	.07
YARTX	$-.48^{d}$	−.16
YARTY	.02	−.11
SITX	$-.44^{d}$	−.05
SITY	$-.31^{b}$	−.23
HFXTX	$-.52^{d}$	−.18
HFXTY	$-.23^{a}$	−.10
TAIR		$.37^{c}$

$^{a}p \leq 0.200$.
$^{b}p \leq 0.100$
$^{c}p \leq 0.050$.
$^{d}p \leq 0.010$.

C4; see Fig. 1) was $0.054 \pm 0.078\ \text{m·s}^{-1}$. The effects of this exceptionally warm and saline inflow are also evident on the northern side of Browns where salinities at mid-depth and below exceed 34.0, an event which was not duplicated on any other cruise during the 6-yr observation period. Furthermore, it is clear from earlier work (Smith 1983; Fig. 6) that the elevated monthly mean salinities at C1–C3 are consistent with those at C4 in Northeast Channel and not with those at C5 and C6 on the Scotian Shelf off Shelburne (see Fig. 1).

Thus it appears that the late-1979 positive salinity anomalies may be attributed, at least in part, to the presence of a warm-core ring off Northeast Channel. (It should also be noted that the salinity anomaly signals at 15 and 20 m fell sharply negative in November, 1979, with the arrival of the freshwater pulse.) Similarly, the positive S2 anomalies observed in the summer of 1984 are consistent with Brooks' (1987) analysis of a warm-core ring off the Channel mouth in late June 1984, which he associated with the presence of Warm Slope Water in Northeast Channel and Georges Basin. However, the deep inflow of slope water and consequent positive salinity and temperature anomalies off Cape Sable cannot be simply inferred from the presence of a warm-core ring at the Channel mouth. For example, Fig. 11 depicts two instances in which warm tongues of surface water associated with offshore rings extended onshore along the 200-m isobath on the eastern side of Northeast Channel. In late August 1980 (Fig. 11a), this event is associated with clearly negative anomalies at C2 in August and September, whereas in August 1984, the anomalies are clearly positive. Thus satellite imagery alone is not a useful way to monitor inflow events.

Discussion

Seasonal Cycles

Wright et al. (1986) have demonstrated that the longshore component of wind stress is more effective than the cross-shore at driving the depth-averaged current and have favourably compared steady model velocities to the observed low-frequency response of mid-depth currents off Cape Sable to Sable Island stress. However, the mean along-isobath current at C2 is westward, in opposition to the mean longshore stress, and the annual cycle in current is well-defined and out of phase with the weak cycle in wind stress. Therefore the dynamics of the mean and seasonal cycle of currents off Cape Sable do not appear to be controlled by wind but rather by other forces such as an alongshore pressure gradient and/or horizontal gradients in the density field (Smith 1983).

The character of the annual cycles in C2 temperature and salinity are quite different. The amplitude of the temperature signal decreased by a factor of two over the water column while the phase lag increased by 0.7 months. This behaviour suggests a diffusive balance with a cyclic sea surface temperature controlled by air–sea interaction. Specifically, if the temperature field were considered to be horizontally uniform, the periodic steady state diffusion of heat is governed by

$$(3)\quad T_t = KT_{zz};\quad T(0,t) = T_o \cos(\sigma t - \psi_o),$$

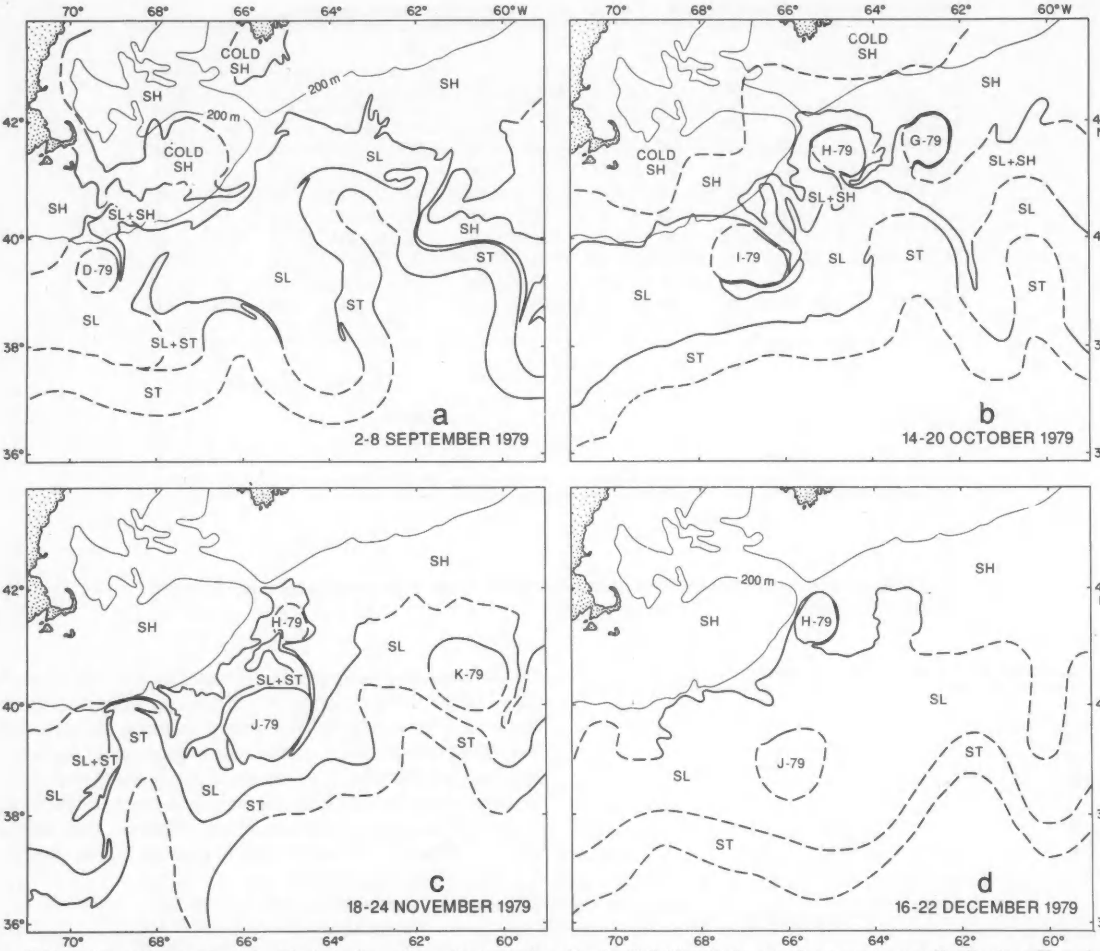

FIG. 9. Experimental ocean frontal analysis (redrawn from charts produced by the U.S. Navy) of sea surface temperature distribution off southwest Nova Scotia. Warm-core rings, shed by the Gulf Stream into the slope water, are labelled by letter codes and their year of formation, e.g. H-79. A dashed contour represents an uncertain frontal position.

where K is the (constant) vertical diffusivity and T_o, ψ_o, and σ are the amplitude, phase, and frequency of the forcing, respectively. The solution to this simple model is

$$(4)\quad T(z,t)=T_o e^{-(\sigma/2K)^{1/2}z}\cos[\sigma t-(\sigma/2K)^{1/2}z-\psi_o],$$

which exhibits the observed decay of amplitude and a linear increase of phase with depth. In an attempt to quantify these results, the amplitudes of the near-surface and bottom annual temperature cycles at C2 and C1 (Tables 1 and 2) were used to evaluate (separately) the two free constants, T_o and K, in equation (4) and the 15-m phase was used to set ψ_o. The results (Fig. 12) show good agreement with the independent estimates of amplitude and phase at other depths (except the spatially-averaged surface values, SST). Furthermore, the vertical gradient of the semiannual phase is larger than for the annual signal, but by a factor of three rather than $\sqrt{2}$ as the theory would suggest. The estimated vertical diffusivities, K, are an order of magnitude smaller than the vertical eddy viscosities derived by Smith (1983) or the vertical diffusivity on nearby Browns Bank (Loder et al. 1988). But the present values are also a factor of 10 larger than those derived by Bugden (1981) and Mountain and Jessen (1987) from their box models for the Gulf of St. Lawrence and Gulf of Maine. Loder and Greenberg (1986) show spatial variations of two orders of magnitude in their vertical mixing parameter (h/D_t) in the Cape Sable region, so perhaps the differences in these estimates is not unrealistic.

A more critical problem with the diffusive model is that the assumption of horizontal homogeneity is obviously violated, so that differential advection may play an important role in maintaining the stratification (van Aken 1986). In fact, using the mean cross-isobath velocities and temperatures to estimate advective heat flux between C1 and C2 gives

$$u\,T_x \simeq 2.5\times10^{-6}\,°\mathrm{C}\cdot\mathrm{s}^{-1} \geq T_t \cong \sigma T_0 \cong 10^{-6}\,°\mathrm{C}\cdot s^{-1}.$$

Thus, despite its success in fitting the annual cycles a C1 and C2, the vertical diffusion model is not consistent internally or with other data from the region.

Advective effects are more evident in the C2 salinity cycle, whose amplitude achieves a maximum at mid-depth. Using historical hydrographic data, Sutcliffe et al. (1976) traced a

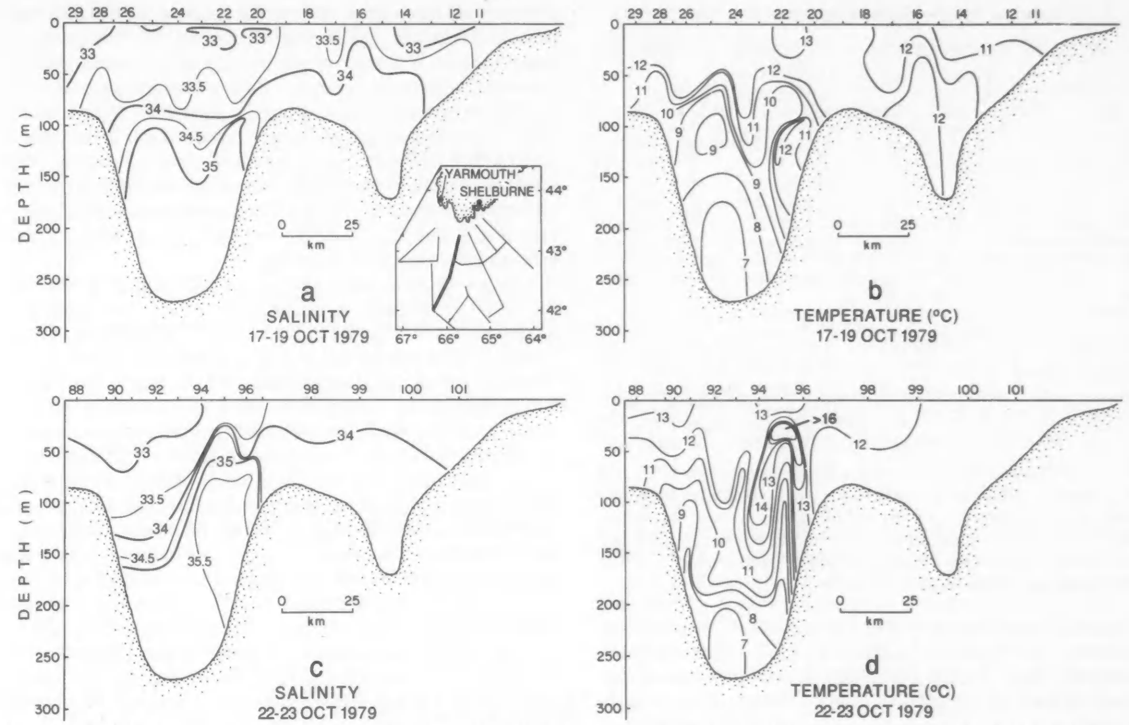

FIG. 10. Repeated temperature and salinity sections from Cape Sable to Georges Bank during October, 1979. (a) salinity, 17–19 October; (b) temperature, 17–19 October; (c) salinity, 22–23 October; (d) temperature, 22–23 October.

16

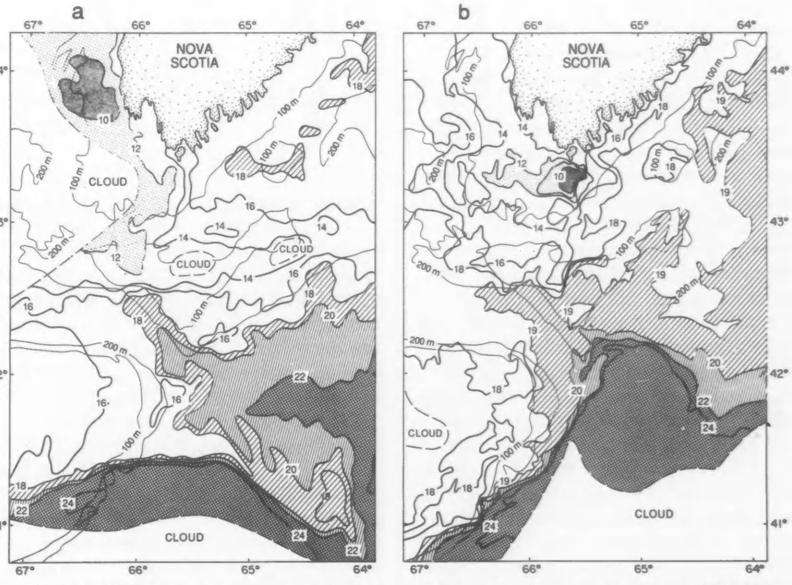

FIG. 11. Sea surface temperature analyses based on satellite infrared imagery (courtesy of the Hydrometeorology Division, Atmospheric Environment Service, Downsview, Ontario). Shaded areas depict warm tongues from warm-core rings entering the eastern side of Northeast Channel and the cold shelf water patches off southwest Nova Scotia.

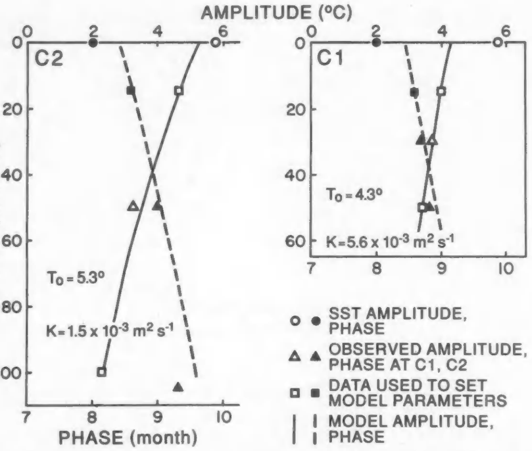

FIG. 12. Diffusion model fit to annual temperature cycles at C2 and C1. Triangles and squares represent observed amplitude (open) and phase (solid) at moorings; circles are for spatial-average sea surface temperature (SST); continuous curves are model amplitude (solid) and phase (dash). Squares were used to set model parameters (T_o, ψ_o and K); triangles are independent observations.

near-surface salinity minimum at speeds of order 7 km·d^{-1} over a distance of 1300 km from the Gulf of St. Lawrence to the Scotian Shelf off Halifax. The phases of the C2 and C1 annual signals indicate that the surface salinity minimum occurs in early February off Cape Sable. Hence the lag between the mid-May peak in freshwater runoff (Fig. 4) and salinity minimum off Cape Sable is 8.5 mo, which implies a reasonable average advection velocity of 6 km·d^{-1} over a total distance of 1500 km. Furthermore, the lag is greater at depth than at the surface, which is consistent with an average vertical shear in the coastal current that transports the freshwater signal. However, this effect is difficult to quantify because of (1) the large error bars on the phase estimates, (2) the difference between vertical phase lags a C1 and C2, and (3) the lack of an accurate and independent measure of the shear.

Another problem with the C2 salinity signal is that the secondary runoff peak, associated with the semiannual cycle in RIVSUM, is not reflected in the surface salinity data in July as expected. This may be due to masking by local effects, winter mixing or other upstream sources such as runoff from Nova Scotia rivers or the melting of the seasonal ice cover in the Gulf of St. Lawrence. While the contributions from upstream sources are estimated to be small, one local influence which might have a significant effect on the Cape Sable annual cycles is the seasonal inflow of slope water through Northeast Channel (Ramp et al. 1985). Even if there were no change in the slope water properties, the late-summer onshore transport maximum would represent enhanced heat and salt fluxes to the deep waters of the outer Gulf which could extend to Cape Sable via the tidally-rectified mean current, for example (Smith 1983). Hydrographic observations of deep water properties in Northeast Channel and Georges Basin do, in fact, show evidence for late-summer/fall maxima in heat and salt content

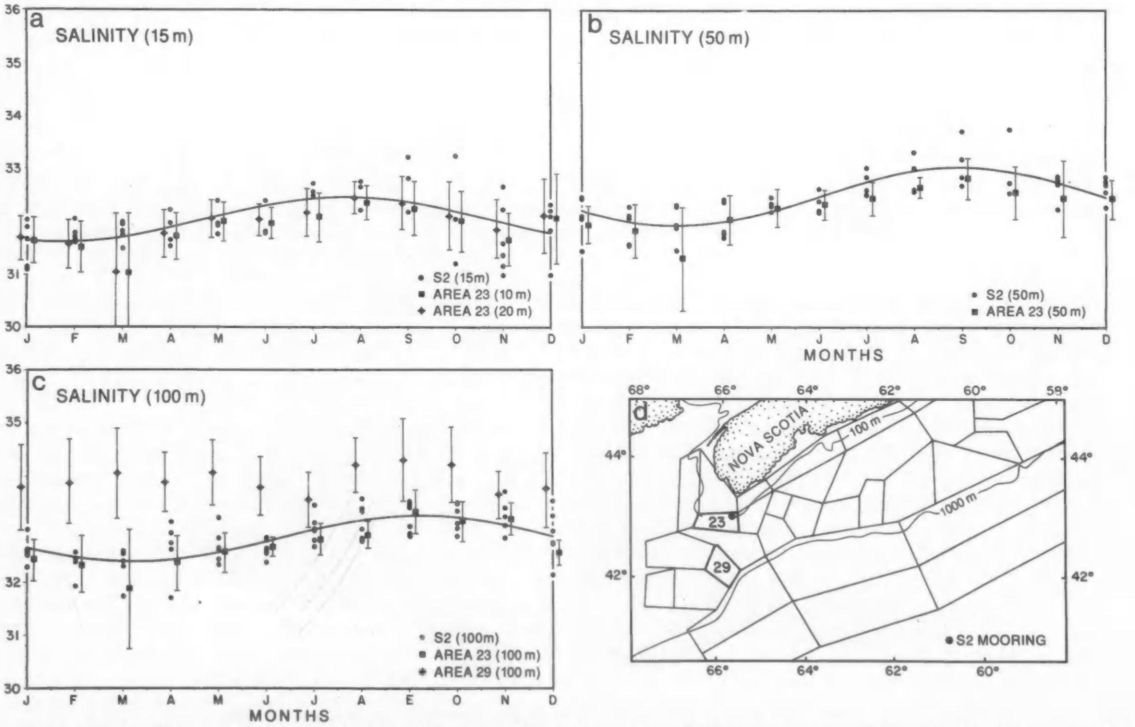

FIG. 13. Comparison between C2 and historical monthly mean salinity observations. The long-term means and standard deviations are taken from Drinkwater and Trites (1987) subareas 23 (Roseway Channel) and 29 (Northeast Channel) based on all CTD and hydrographic bottle data from the archives of the Marine Environmental Data Service (MEDS).

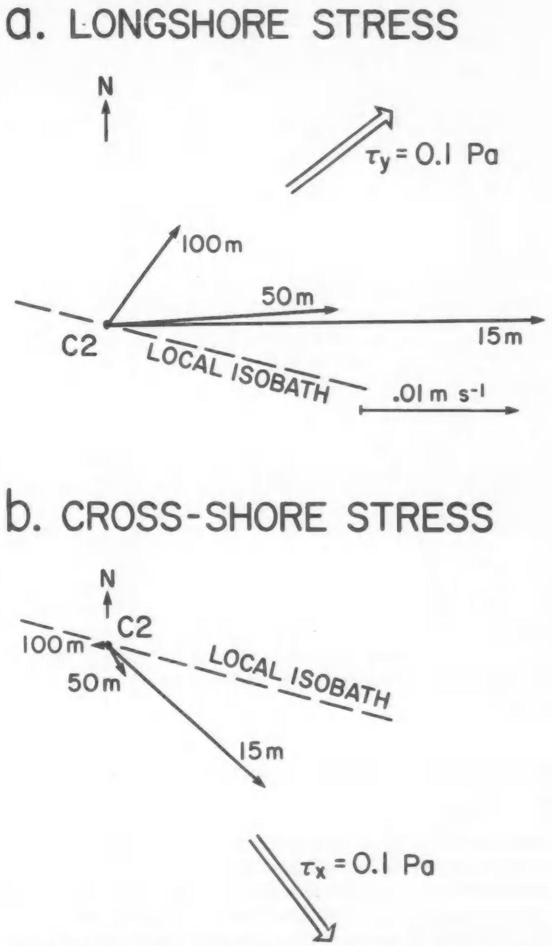

FIG. 14. Responses of C2 currents to 0.1 Pa longshore (a) and cross-shore (b) wind stresses.

TABLE 7. Mean and annual cycles for Roseway Channel (subarea 23) and C2 salinities.

	Subarea 23			C2		
	Mean	AMP*	Phase*	Mean	AMP*	Phase*
S(10 m)	31.85	0.39±0.07	7.8±0.4			
S(15 m)				32.04	0.43±0.18	7.2±0.8
S(20 m)	31.94	0.43±0.07	7.9±0.3			
S(50 m)	32.24	0.50±0.06	8.3±0.2	32.47	0.55±0.13	8.5±0.4
S(100 m)	32.67	0.51±0.06	8.6±02	32.81	0.43±0.11	8.7±0.5

*95% Confidence limits are computed as in Table 1, except the standard error of the mean replaces the standard deviation of the residual.

(Mountain and Jessen 1987). Moreover, long-term average salinities at 100 m in Northeast Channel are generally 1 to 2 psu higher than at C2(100 m), and exhibit a weak September maximum coincident with that at C2 (Fig. 13c). The historical data were compiled by the Marine Environmental Data Service (MEDS) by averaging all available hydrographic observations between 1914 and 1986 in subareas defined by Drinkwater and Trites (1987) for the Scotian Shelf region. Regression analysis (1) indicates that the annual cycle of the 100 m salinity in Northeast Channel (subarea 29) is not significant, but that the mean value (based on 339 samples) is 1.1 psu higher than the 6.5-yr mean at C2(100 m).

Figure 13 also compares the long-term monthly mean salinities at instrument depths in Roseway Channel (subarea 23, which contains the C2 site) against the C2 monthly means and annual cycles. Regression analysis (1) of the Roseway Channel data indicates that the mean salinities are slightly smaller than those from C2, but that within the estimated uncertainty, the amplitudes and phases of the significant annual cycles are equivalent (Table 7). Furthermore, part of the discrepancy may be caused by some anomalously low salinities ($S \cong 27.1, 30.0, 30.2$ at depth = 0, 50, 100 m) included in the historical March data. Removal of the March averages raises mean salinities by 0.05 while reducing the surface amplitude and phase by 0.10 and 0.2, respectively.

Anomalies

Unlike the mean and annual cycles, the high correlations with Yarmouth wind stress suggest that the C2 current anomalies are largely wind driven. To quantify this relationship, the regression coefficients and standard deviations of the C2 current components versus YARTY and YARTX have been used to calculate the oceanic responses to longshore and cross-shore stresses of 0.1 Pa (Fig. 14). As expected, the current response to longshore stress is greater at all depths and consistent with Ekman dynamics in the sense that the surface (bottom) current is rotated offshore (onshore) with respect to the mid-depth velocity for positive longshore stress. The mid-depth response is in the same direction but somewhat smaller than that found by Wright et al. (1986) based on linear regression in the spectral domain. (This difference is especially surprising since they used the more energetic Sable Island stress forcing.) However, the present analysis is based on data from all seasons, whereas Wright et al. (1986) used winter data only. Noble et al. (1985) found reduced transfer coefficients in late summer on Georges Bank with overall average mid-depth values of order $0.2\ \mathrm{m\cdot s^{-1}\cdot Pa^{-1}}$, comparable with that in Fig. 14.

The response to cross-shore wind stress is weaker than to longshore stress and concentrated in the surface layer. This is also qualitatively consistent with Ekman dynamics since the Ekman mass flux in the alongshore direction would fail to create a coastal divergence and cross-shore pressure gradient to drive deep currents. However, the near-surface response is roughly aligned with the wind rather than rotated clockwise in the classical Ekman sense. This effect may be lost in the noise or absent because the geometry is not simply two-dimensional.

The positive correlations between YARTY and the deep temperature and salinity anomalies are also consistent with wind-driven upwelling. Positive longshore stress causes upwelling of warmer, saltier deep water; negative stress causes downwelling of cooler, fresher water from the cold intermediate layer. The correlation persists at mid-depth for salinity but not for temperature because the salinity increases monotonically with depth whereas the temperature profile in summer may have a mid-depth minimum.

On a somewhat larger scale, the wind stress correlation with temperature and salinity may reflect the wind-driven response of the outer Gulf of Maine. Ramp et al. (1985) demonstrated that longshore wind is positively correlated with deep winter

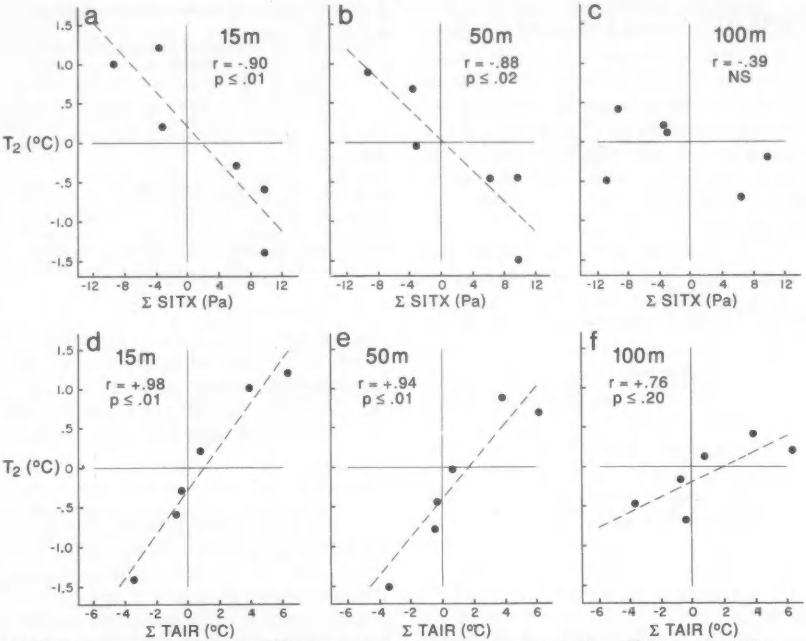

FIG. 15. Comparison of February C2 temperature residuals to total wintertime (Σ November-February) cross-shore wind stress (SITX) and air temperature (TAIR) anomalies. Dashed lines show linear regressions with coefficients, *r*, and indicated significance levels.

inflow through Northeast Channel. The inflow, they suggest, is driven by the onshore pressure gradient associated with sea level set-down at the coast. Model results of Wright et al. (1986) also show enhanced inflow in response to positive longshore stress. The present results suggest that warm saline water carried by this inflow may be advected toward the Scotian Shelf and upwelled off Cape Sable by the same wind-driven circulation. Thus the strong positive (negative) T,S anomalies in the late fall of 1979 (winter of 1982/83) are also periods of positive (negative) longshore wind stress anomaly. However, similar correspondence is not found for the positive (negative) anomalies of the winter of 1982/82 (1983/84). Furthermore, the influence of warm-core rings in the slope water may be felt in the absence of any significant wind forcing, as described by Brooks (1987) for events in June 1984 and 1986. Thus the wind-driven mechanism appears to be only one of several processes controlling the water properties off Cape Sable.

Although the phases of the annual cycles of RIVSUM and C2 salinities are consistent with advection of the freshwater pulse by coastal currents, the failure to find significant negative correlations at lags of 8 to 9 mo suggests that the RIVSUM anomalies are effectively masked by local or other upstream effects. Furthermore, the correlations between C2 temperatures and RIVSUM at lags of 7 to 9 mo (Table 5) are inconsistent with Sutcliffe et al. (1976), who associated increased runoff with positive temperature anomalies in the surface layer. The failure to find significant correlations between RIVSUM and temperature is consistent with the results of Koslow et al. (1986). However, it should be pointed out that the Sutcliffe analysis was more refined than this one in the sense that the former was separated by month so that correlations in critical months could be identified. The present method weights all months equally. Furthermore, most of the variance in the Sutcliffe data was at periods of 10–20 yr (K. Drinkwater, Physical and Chemical Sciences, Bedford Institute of Oceanography, Dartmouth, N.S., pers. comm.). Thus some of the interannual signal would be lost in a 6.5-yr data set. However, Fig. 13 indicates that the ranges of C2 monthly means about the annual cycles are comparable with the standard deviations of the historical means (which contain both spatial and temporal variabilities). Therefore, in this region and time frame, C2 monthly time series provide a reasonable measure of the interannual variability.

Finally, Thompson et al. (1988) have attributed large-scale wintertime sea surface temperature variability in this region to interannual fluctuations in air–sea heat exchange reflected by the strength of the cross-shore wind component. Onshore (offshore) winter winds are usually warm and moist (cold and dry) and cause a marked reduction (increase) in heat loss to the atmosphere. This effect is evident in the strong negative correlations of TAIR and cross-shore stress components and the positive correlation of TAIR and SST (Table 6). The direct correlation of TAIR with near-surface temperature anomalies at C2 (Table 5) is not significant, but it fails to account for the cumulative effect of excess heating (or cooling) over the winter season. Following Thompson et al., the comparison of February C2 temperature anomalies (i.e. approximately at the end of the cooling cycle) with the sum of cross-shore wind stress anomalies at Sable Island over the previous winter (November–February) gives a significant negative correlations at the surface and mid-depth (Fig. 15a,b). Moreover, the February ocean temperature residuals at all depths are correlated with the sum of Halifax air temperature anomalies to some extent (Fig. 15 d–f). Thus the present results not only confirm the conclusions of

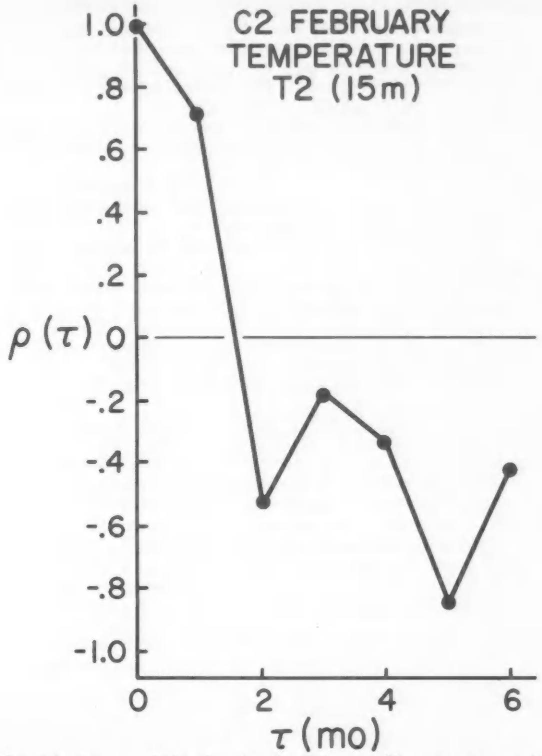

FIG. 16. Autocorrelation function for February C2 temperature residuals at 15 m.

Thompson et al. (1988) that interannual fluctuations in the atmospheric circulation and related heat fluxes control regional sea surface temperature, but also extend that result to at least 50-m temperatures in the waters off southwest Nova Scotia.

On the other hand, the lack of persistence of winter anomalies in the present data set, as indicated by the rapid decorrelation between February surface temperature and the anomalies in subsequent months (Fig. 16), is inconsistent with Thompson et al.'s long-term observations and stochastic model for the mixed-layer temperature anomalies. It may be that the mixed-layer depth in the strong tidal regime is controlled differently than on the open shelf, or that the present data set is too short to evaluate the seasonally-dependent autocorrelation function.

Summary and Conclusions

A multiple regression technique has been used to determine the following characteristics of the mean and seasonal cycles in 6.5 yr of oceanographic and related data off southwest Nova Scotia: (1) At C2 on the 110-m isobath, strong annual signals are found in temperature, salinity, and along-isobath velocity at all depths. A significant semiannual signal in temperature also reinforces the late summer maxima at 15 and 50 m depth. At C1 on the 60-m isobath, temperature and salinity cycles are similar, but the cross-isobath rather than along-isobath component of current shows the dominant annual signal. (2) The cross-shore wind stress components at Yarmouth, Halifax and Sable Island exhibit strong annual signals, whereas the longshore signal is weak and out of phase with the C2 along-isobath current. Moreover, the mean longshore stress opposes the mean current. This suggests that longshore wind is not the dominant forcing mechanism for the mean along-isobath current and its seasonal cycle. (3) Freshwater runoff into the Gulf of St. Lawrence (RIVSUM) has comparable annual and semiannual signals. The phase of the annual RIVSUM maximum in mid-May is consistent with the arrival of a salinity minimum off Cape Sable in early February with an average advection speed of 6 km·d^{-1}, but there is no evidence for a secondary minimum corresponding to the fall runoff peak. The masking of the secondary salinity minimum may be caused by the seasonal variation of slope water input to the Gulf of Maine via Northeast Channel. The summer inflow maximum would reinforce the cycle associated with the spring peak in RIVSUM but conflict with that induced by the fall peak. (4) A simple vertical diffusion model, forced at the surface, is capable of fitting the observed amplitudes and phases of the annual cycles of temperature. The inferred diffusivities are reasonably consistent with other local estimates, but the neglect of horizontal heat transport in the model is not justified.

From correlations of the residual time series, the following conclusions are also derived: (5) in spite of the apparent influence of RIVSUM on the annual cycle in salinity off Cape Sable, RIVSUM anomalies are not negatively correlated with C2 salinity residuals at the expected 8–9 mo lag. (6) The strong correlations between longshore stress and currents, deep salinity, and temperature are consistent with Ekman dynamics and wind-driven upwelling. This suggests that atmospheric circulation, not runoff, may control salinity anomalies. Following Ramp et al. (1985) and the model results of Wright et al. (1986), positive longshore stress enhances slope water inflow through Northeast Channel and may induce positive heat and salt fluxes to the Cape Sable region. (7) The presence of Gulf Stream warm-core rings at the mouth of Northeast Channel sometimes produces warm, saline anomalies off Cape Sable, but satellite imagery alone is not a reliable indicator of this process. (8) February temperature anomalies to at least 50 m are controlled by interannual variability in the winter-average winds and related heat fluxes, but there is no evidence for persistence of these conditions well into the spring, as suggested by Thompson et al. (1988).

Finally, it is worth repeating that, based on a comparison with seasonal cycles and residuals from historical observations, the C2 time series are reasonable indicators of interannual variability off southwest Nova Scotia.

Acknowledgements

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References

ANDERSON, C., AND P. C. SMITH. 1989. Oceanographic observations on the Scotian Shelf during CASP. Atmosphere-Ocean 27(1): 130–156.

BIGELOW, H. B. 1927. Physical oceanography of the Gulf of Maine. U.S. Dept. Comm. Bur. Fish. Bull. 40: 511–1027.

Blanton, J. O., F. B. Schwing, A. H. Weber, L. J. Pietrafesa, D. W. Hayes. 1985. Wind stress climatology in the South Atlantic Bight. *In* Oceanography of the Southeastern U.S. Continental Shelf, Atkinson et al. [ed.] AGU, Washington, D.C. 10–22.

Boyce, R. 1986. Condutivity cell calibration drift of the Aanderaa current meter. Can. Tech. Rep. Hydrogr. Ocean Sci., No. 70, 18 p.

Brooks, D. A. 1985. Vernal circulation in the Gulf of Maine. J. Geophys. Res. 90: 4687–4705.

1987. The influence of warm-core rings on slope water entering the Gulf of Maine. J. Geophys. Res. 92: 8183–8196.

Bugden, G. 1981. Salt and heat budgets for the Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 38: 1153–1167.

Butman, B., and R. C. Beardsley. 1987. Long-term observations on the southern flank of Georges Bank. Part I: A description of the seasonal cycle of currents, temperature, stratification and wind stress. J. Phys. Oceanogr. 17: 367–384.

Drinkwater, K. F., and R. W. Trites. 1987. Monthly means of temperature and salinity in the Scotian Shelf region. Can. Tech. Rep. Fish. Aquat. Sci. 1539: iv + 101 p.

Fofonoff, N. B., and H. Bryden. 1975. Specific gravity and density of sea water at atmospheric pressure. J. Mar. Res. 33: 69–82.

Garrett, C. J. R., J. R. Keeley, and D. A. Greenberg. 1978. Tidal mixing versus thermal stratification in the Bay of Fundy and Gulf of Maine. Atmosphere-Ocean 16: 403–423.

Gatien, M. G. 1976. A study in the slope water region south of Halifax. J. Fish. Res. Board Can. 33: 2213–2217.

Hopkins, T. S., and N. Garfield. 1979. Gulf of Maine intermediate water. J. Mar. Res. 37: 103–139.

Koslow, J. A., R. H. Loucks, K. R. Thompson, and R. W. Trites. 1986. Relationships of St. Lawrence River outflow with sea surface temperature and salinity in the Northwest Atlantic. *In* The role of freshwater outflow in coastal marine ecosystems. S. Skreslet [ed.] Springer-Verlag, Berlin.

Lively, R. R. 1984. Current meter, meteorological and sea level observations off Cape Sable, Nova Scotia. Can. Tech. Rep. Hydrogr. Ocean Sci., No. 40, 494 p.

1985. Current meter, meteorological and sea level observations off Cape Sable, Nova Scotia, August 1980 to April 1983. Can. Tech. Rep. Hydrogr. Ocean Sci., No. 66, 528 p.

Loder, J. W., and D. A. Greenberg. 1986. Predicted positions of tidal fronts in the Gulf of Maine region. Cont. Shelf Res. 6: 397–414.

Loder, J. W., C. K. Ross, and P. C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. 45: 1860–1885.

Mountain, D. G., and P. A. Jessen. 1987. Bottom waters of the Gulf of Maine, 1978–1983. J. Mar. Res. 45: 319–345.

Myers, R. A., S. A. Akenhead, and K. Drinkwater. 1990. The influence of ice-melt and Hudson Bay runoff on the salinity of the Newfoundland Shelf. Atmosphere-Ocean 28: (In press)

Noble, M. A., B. Butman, and M. Wimbush. 1985. Wind-driven current coupling on the southern flank of Georges Bank: variation with season and frequency. J. Phys. Oceanogr. 15: 604–620.

Ramp, S. R., R. J. Schlitz, and W. R. Wright. 1985. The deep flow through the Northeast Channel, Gulf of Maine. J. Phys. Oceanogr. 15: 1790–1808.

Smith, P. C. 1983. Mean and seasonal circulation off southwest Nova Scotia. J. Phys. Oceanogr. 13: 1034–1054.

1987. The distribution of surface wind over the Scotian Shelf. *In* Proceedings of the International Workshop on Wave Hindcasting and Forecasting. Environ. Stud. Rev. Funds, Rep. No. 065, 25–36.

1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

Smith, P. C., R. R. Lively, and K. C. Brown. 1984. An intercomparison of near-surface measurements with Aanderaa and AMF VACM current meters in strong tidal currents. Can. Tech. Rep. Hydrogr. Ocean Sci. 48: 36 p.

Smith, S. D., and E. G. Banke. 1975. Variation of sea surface drag coefficient with wind speed. Quart J. Roy. Meteor. Soc. 101: 665–673.

Sutcliffe, W. H., Jr., R. H. Loucks, and K. F. Drinkwater. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and Gulf of Maine. J. Fish. Res. Board Can. 33: 98–115.

Tee, K. T., P. C. Smith, and D. Lefaivre. 1988. On the estimation and verification of tidally-induced residual currents. J. Phys. Oceanogr. 18: 1415–1434.

Thompson, K. R., R. H. Loucks, and R. W. Trites. 1988. Sea surface temperature variability in the shelf-slope region of the northwest Atlantic. Atmosphere-Ocean 26: 282–299.

vanAken, H. M. 1986. The onset of seasonal stratification in shelf seas due to differential advection in the presence of a salinity gradient. Cont. Shelf. Res. 5: 475–485.

Wright, D. G., D. A. Greenberg, J. W. Loder, and P. C. Smith. 1986. The steady-state response of the Gulf of Maine and adjacent regions to surface wind stress. J. Phys. Oceanogr. 16: 947–966.

Particle Drift in the Surface Layer off Southwest Nova Scotia: Description and Evaluation of a Model[1]

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Page, F. H., and P. C. Smith. 1989. Particle drift in the surface layer off southwest Nova Scotia: description and evaluation of a model. Can. J. Fish. Aquat. Sci. 46(Suppl.1): 21–43.

A two-dimensional (horizontal) surface layer particle dispersion model for the Southwest Nova Scotia region is described and evaluated. The model is based on a barotropic M_2 tidal model and wind-driven response model. It includes a constant residual current field plus time varying M_2 tidal and wind-driven currents. Tidal currents are shown to cause particle trajectories to vary with the time of particle release. Constant winds are shown to have an important influence on particle trajectories, although periodic winds have little effect. Comparisons between simulated particle trajectories and satellite-tracked drogue trajectories show the model can qualitatively reproduce drogue trajectories on the western, but not on the eastern portion of Browns Bank. However, the model consistently underestimates the observed displacements. These discrepancies are probably due to (1) unmodelled baroclinic components of the circulation and/or (2) the inability of the model to resolve strong topographic gradients and the resulting rectified currents over the steep flanks of the Bank. The use of a previous empirically-defined circulation does not significantly improve the model's performance.

Nous décrivons et évaluons un modèle bidimensionnel (horizontal) de la dispersion des particules dans la couche superficielle pour la région du sud-ouest de la Nouvelle-Écosse. Ce modèle se fonde sur un modèle barotrope de la marée M_2 et sur un modèle de la réaction au vent. Il comporte un champ résiduel de courant constant plus des courants de la marée M_2 et des courants de vent variant avec le temps. Nous montrons que les courants de marée ont pour effet de faire varier la trajectoire des particules en fonction du moment de leur émission. Les vents constants ont une influence importante sur la trajectoire des particules, alors que celle des vents périodiques est faible. Les comparaisons entre les trajectoires simulées des particules et les trajectoires de drogues suivies par satellites montrent que le modèle peut reproduire qualitativement le déplacement des drogues sur la partie ouest mais non sur la partie est du banc de Browns. Le modèle sous-estime toutefois de façon constante les déplacements. Ces écarts sont probablement dus (1) aux éléments baroclines non modélisés de la circulation et/ou (2) à l'inaptitude du modèle à intégrer les forts gradients de la topographie et les courants rectifiés qui en résultent sur les flancs abrupts du banc. Le recours à une circulation définie précédemment de façon empirique n'améliore pas nettement le rendement du modèle.

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Knowledge of the dispersal patterns of fish eggs and larvae is of fundamental importance to fisheries biology and management. Dispersal patterns are believed to influence stock structure (i.e. discreteness, unity, and number: Harden-Jones 1965, 1968; Cushing 1975, 1981; Iles and Sinclair 1982) and year-class size (Hjort 1914; Iles and Sinclair 1982) through the transport and dispersion of early life stages. Unfortunately, the evidence needed to test and refine these beliefs is difficult to obtain. Ichthyoplankton surveys are expensive, and because the eggs and larvae are distributed over large spatial scales, of order 100 km, the surveys are nonsynoptic. Therefore advective and diffusive fluxes must often be estimated from either empirical relationships relating physical variables to year-class size (e.g. Carruthers et al. 1951a,b; Chase 1955; Nelson et al. 1977; Bailey 1981; Sinclair et al. 1985) or from simulations with physical circulation models (e.g. Bartsch 1988).

Validation of the indices and model results is hindered by the low numbers and high variance of observations describing the dispersion patterns. Confidence therefore depends on the reliability of the underlying assumptions and the accurate representation of the component mechanisms. Circulation models are usually tested in an Eulerian framework, that is, by comparing model and observed currents at fixed locations, in spite of the fact that it is the Lagrangian circulation that governs the dispersion patterns. In the few cases where Lagrangian validations have been attempted, the models were usually qualitatively but not quantitatively satisfactory (e.g. Trites et al. 1986).

The Southwest Nova Scotia Fisheries Ecology Program (FEP) was initiated in 1983 to investigate the haddock stock

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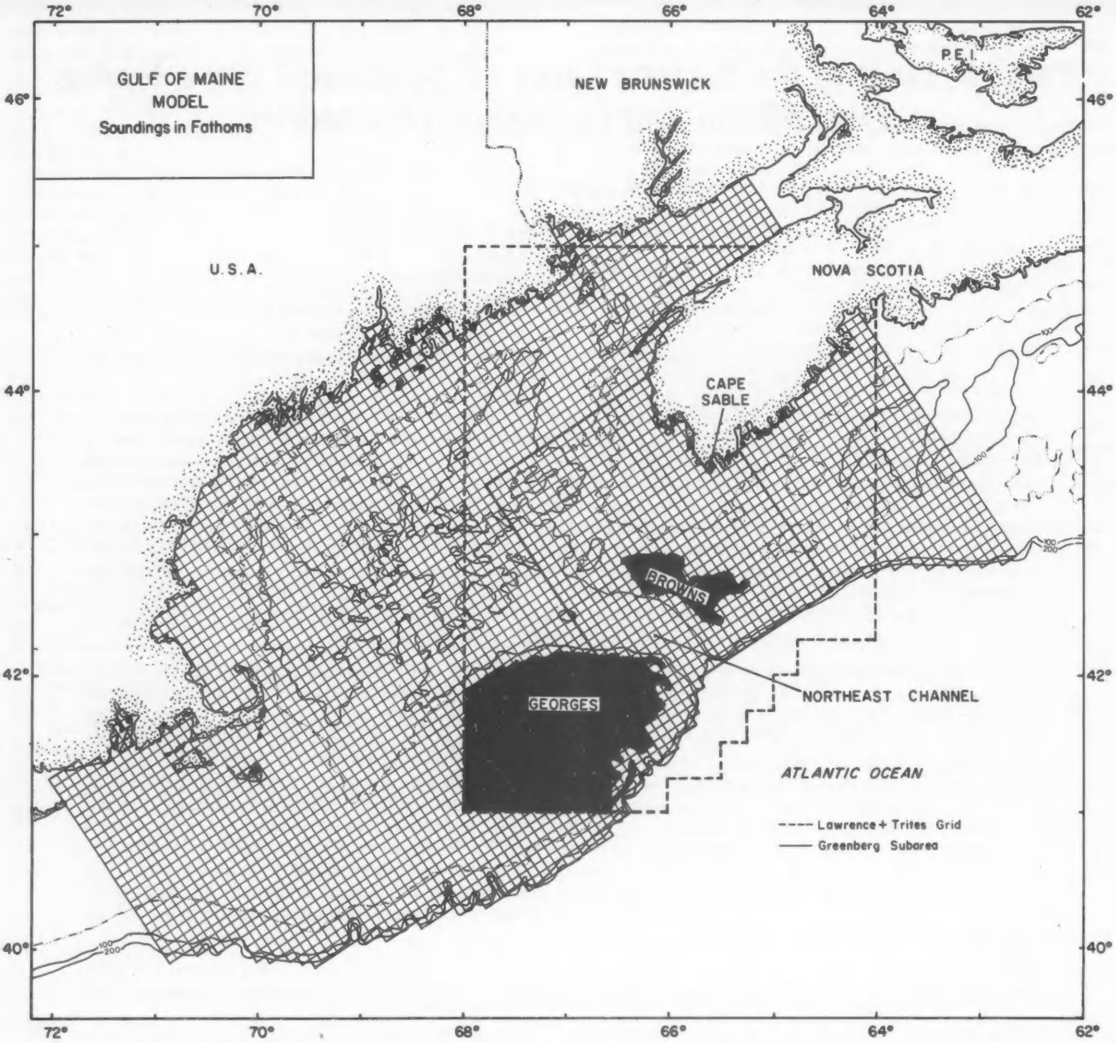


FIG. 1. Location map showing the perimeters of the Lawrence and Trites (1983; dashed line) and Greenberg (1983; bold solid line) subgrids superimposed on the full Greenberg (1983) grid.

which resides in the Southwest Nova Scotia region. The principal spawning ground is over Browns Bank (Fig. 1), although spawning may also occur on adjacent banks or near the mouth of the Bay of Fundy. Spawning takes place from March through May, with peak spawning occurring in April and early May (Page and Frank 1989), but to date no definitive evidence for subsequent advection and dispersion of the haddock eggs and (planktonic) larvae in this region has emerged.

Historically, two schools of thought have arisen regarding the fate of haddock ichthyoplankton. Early observations suggested the eggs and larvae drifted with the nontidal residual circulation from Browns Bank toward the mouth of the Bay of Fundy (Bigelow 1926, 1927). This interpretation is supported by observations on the seasonal evolution of the distribution of the pteropod, *Limacina retroversa* (Redfield 1939).

More extensive observations on the distribution of haddock eggs, larvae, and demersal juveniles (Walford 1938; Marak and Colton 1961; Marak et al. 1962a,b; Colton 1965) and on the surface circulation (Walford 1938; Day 1958; Bumpus and Lauzier 1965), were conducted during the 1930's to 1960's. Unfortunately, the ichthyoplankton surveys were unable to resolve the displacements during the egg and larval stages since the surveys only covered the area to the west of Browns Bank and they used sampling gear which does not representatively capture the larvae. Evidence for the direction of the larval drift therefore came largely from the distribution of juveniles. The rate of this drift remained uncertain, although surface drift bottles released over Browns Bank suggested a net speed of approximately 5 km/d toward the inshore and the Bay of Fundy.

During the late 1970's and early 1980's ichthyoplankton (O'Boyle et al. 1984; Koslow et al. 1985) and juvenile (Scott 1982; Koeller et al. 1986) surveys sampled the entire Southwest Nova Scotia region and used sampling gear (bongo nets) which reliably captured both the eggs and young larvae (<10 mm in length). Collocation of the observed distributions of haddock eggs and larvae led O'Boyle et al. (1984) to the conclusion that these ichthyoplankton were physically retained over Browns Bank and thus, contrary to the dogma of larval drift, the haddock spawning and nursery grounds were not spatially separated. They also suggested that this retention was qualitatively consistent with the existence of the newly-discovered residual gyre on Browns Bank (Smith 1983; Greenberg 1983).

In an effort to help resolve this controversy between drift and retention, a Lagrangian particle tracking model capable of estimating the patterns of haddock egg and larval dispersion has been developed as part of the FEP. The intention is to use this model to help interpret the observed distributions and perhaps suggest simple dispersion indices which could be compared with estimates of the recruitment variation.

The core of any Lagrangian model is an accurate (Eulerian) representation of the circulation. The Southwest Nova Scotia region has been well studied from a physical oceanographic viewpoint (Bigelow 1927; Day 1958; Smith 1983, 1989a,b) and numerical models of the tidal, residual (Greenberg 1983; Tee et al. 1987), and wind-driven circulations (Wright et al. 1986) are available. The Eulerian currents, measured at fixed locations on Browns Bank, are highly variable, with the variance in many locations exceeding the mean by a factor of 10 or more (Loder et al. 1988). Furthermore, root-mean-square excursions associated with the fluctuating currents are comparable with the length scales of the mean shear, particularly near the surface. Under these circumstances, the Lagrangian circulation governing the particle trajectories may be quite different from that inferred from the Eulerian residual currents (Longuet-Higgins 1969; Zimmerman 1979; Cheng et al. 1986). Therefore the relationship between the mean circulation and the displacements of haddock eggs and larvae is uncertain.

The two-dimensional model developed for the surface layer off Nova Scotia includes time-varying tidal and wind-induced currents in addition to the mean currents. The purpose of this paper is to describe the model, evaluate the importance of the time-varying tidal and wind-driven components of the circulation in determining particle trajectories, and assess the model's utility by comparing predicted particle paths with the observed trajectories of satellite-tracked drogues.

Materials and Methods

Model Overview

Assuming linear superposition of the various components of the circulation, Eulerian horizontal velocities $[u(x,y,t), v(x,y,t)]$ are specified at evenly spaced grid points as,

$$u = U + A_x \cos(\omega t - P_x) + \tau_x G_{xu} + \tau_y G_{yu}$$
$$v = V + A_y \cos(\omega t - P_y) + \tau_x G_{xv} + \tau_y G_{yv}$$

where $U(x,y), V(x,y)$ are the components of the residual (mean) velocity along the x- and y-axes, $A_x(x,y)$, $A_y(x,y)$ are the M_2 tidal amplitudes, $P_x(x,y)$, $P_y(x,y)$ are the tidal phases, $\omega = 2\pi/T$ and T are the M_2 tidal frequency and period (assumed to be 12.5 h), $\tau_x(t)$, $\tau_y(t)$ are the (uniform) components of the surface wind stress, and G_{xu}, G_{xv} (G_{yu}, G_{yv}) are the spatially-varying gain factors relating $\tau_x(\tau_y)$ to the u and v components of the wind-driven current. U, V, A_x, A_y, P_x, P_y, G_{xu}, G_{xv}, G_{yu}, G_{yv} have previously been computed from Greenberg's barotropic 2-D model on a Richardson lattice (Greenberg 1983; Wright et al. 1986). τ_x and τ_y are sea surface wind stress components estimated from hourly wind measurements at Sable Island (Smith 1989b).

In order to estimate the trajectories of particles from the Eulerian velocity field, an iterative Lagrangian particle-tracking technique was adopted (e.g. Forrester 1973; Hunter 1987). At the beginning of each time step, the velocity at the particle position is calculated and the new position is estimated from

(1) $\mathbf{p}(t+dt) = \mathbf{p}(t) + \mathbf{u}[\mathbf{p}(t), t]\, dt,$

in which $\mathbf{p}(t)$ is the position vector at time t, $\mathbf{u}[\mathbf{p}(t), t]$ is the velocity vector at position $\mathbf{p}(t)$ and time t (i.e. the position at the beginning of each time step) and dt is the time step. In order to reduce displacement errors generated by spatial and temporal gradients in the Eurlerian velocity field, the velocity at the projected position $\{\mathbf{u}[\mathbf{p}(t+dt), t+dt]\}$ is averaged with the velocity at the initial position and a revised estimate of the new particle position is made using this average velocity according to,

(2) $\mathbf{p}(t+dt) = \mathbf{p}(t) + \{\mathbf{u}[\mathbf{p}(t), t] + \mathbf{u}[\mathbf{p}(t+dt), t+dt]\}\, dt/2$

This procedure is iterated until the average velocity changes by less than 0.1 cm/s. This scheme is stable for $dt < 2/|d\mathbf{u}/d\mathbf{x}|_{\max}$ (Hunter 1987). In all cases the Eulerian velocities were interpolated to particle positions using a six point bi-variate interpolation scheme (Abramowitz and Stegun 1964; Press et al. 1986), with due regard to the definition of the velocity components on the Richardson lattice (Greenberg 1983).

The computer program implementing the above scheme was written in BASICA and run on a 640K Panasonic Business Partner FX-600 personal computer equipped with an 8087-2 co-processor chip and two 360K disk drives. When tidal motions were included in the model a time step of 0.5 h and an iteration accuracy of 0.1 cm/s was found to give adequate results (see model check in Results section).

Flow Field Specification: Residual

We have used two approaches to define the residual velocity field. Our first approach, following that often used in oil spill trajectory modelling (e.g. Spaulding et al. 1983; Lawrence and Trites 1983; Trites et al. 1986), employs the empirically-defined seasonal (winter and summer) velocity fields compiled by Lawrence and Trites (1983) for the Gulf of Maine. These velocities were estimated on a 1/4° × 1/4°grid (latitude × longitude) from a wide range of information, including current meter records, drift bottle returns, satellite-tracked drifter trajectories, and geostrophic calculations. Since we are primarily interested in the circulation during the haddock spawning season of March through May, the annual average velocity vectors $[(V_{\text{sum}} + V_{\text{win}})/2]$ were used as the residual velocity field. This approach has the advantage that all components of the residual current (barotropic and baroclinic) are included in the estimates. The disadvantages are that errors in those estimates may render the flow horizontally divergent and interannual variation in the residual current cannot be incorporated. Also, since the grid scale (approximately 20×28 km) is of the same order as the topographic length scale characterizing Browns Bank, the detailed circulation there is poorly resolved.

In order to achieve a greater spatial resolution and to ensure a dynamically consistent flow field, we also use the residual currents predicted by the nonlinear barotropic M_2 tidal model of Greenberg (1983). This depth-averaged model computes Eulerian residuals for the entire Gulf of Maine, Bay of Fundy, and western Scotian Shelf regions based on sea level calibrations of the tide at various coastal and offshore stations. Only the Southwest Nova Scotia portion of this model is used (Fig. 1). The x-(36 grid points) and y-(25 grid points) axes are oriented in the cross-shore (146°*T*) and along-shore (56°*T*) directions, respectively, with equal resolutions of $dx = dy = 7.25$ km.

The residual currents generated by the Greenberg model are similar to those generated by the three-dimensional tidal models of Isaji and Spaulding (1984) and Tee et al. (1987), but the agreement between modelled and observed tidal residual velocities is variable. In particular, Tee et al. (1987) found their 3-D tidally-induced velocities agree with those observed to within roughly 50% in the inshore region near Cape Sable, but around the edges of Browns Bank, the model underestimates the observations by a factor of approximately four at the surface. This discrepancy has been attributed to the inability of the 7-km grid to resolve the bottom topography defining the Bank. In the inshore region between Halifax and Cape Sable, Tee et al.'s model also underestimates the observed velocities, but the magnitude of this difference is uncertain due to large spatial variation in the predicted velocities and to large error bars on the observed values (Tee et al. 1987).

Another disadvantage of the Greenberg model is that baroclinic components of the circulation, particularly over Browns Bank and in the Nova Scotian Current inflow, are not included. Smith (1983) attempted to account for the depth-averaged component of the Scotian Shelf inflow by adding a pressure driven current generated by a coastal set-up in sea level along the eastern boundary at Halifax. He found best agreement with observations using a linearized version of the Greenberg model with either a 4-cm set-up at Halifax which decays exponentially offshore or a 2-cm Halifax set-up which decays linearly to the shelf edge. The former boundary condition serves to concentrate the inflow currents nearer the coast, but the net alongshore transports are equivalent (Wright et al. 1986).

Flow Field Specification: Time-Varying Flow

Tidal currents are estimated using the amplitudes and phases predicted by the Greenberg (1983) model. Comparisons with observations in various regions have indicated that tidal currents are accurately estimated by the model. In the shallow waters on the northern flank of Georges Bank the model M_2 amplitudes and phases are within 5% and four degrees, respectively of values estimated from current meter records (Marsden 1986). At a location in the deeper waters just off the northern flank the discrepancy increases to 10–35% in amplitude and 6–91 degrees in phase (Marsden 1986). This reduction in accuracy may, however, be due to mooring motion or a baroclinic tide since the predicted values are in close agreement with theoretical expectations (Marsden 1986). Off Cape Sable, both the depth-averaged component and vertical structure of the model M_2 tidal currents are in close agreement with observations (Tee et al. 1987).

The current variation with periods of 2 to 10 d is largely driven by the wind (Smith 1989a) and can be estimated, for the lowest frequencies at least, using the steady-state model wind-current gains of Wright et al. (1986). Since these gains apply to the depth-averaged current, they agree most favourably with those measured at mid-depth current meters. The observed low-frequency response near the surface (bottom) is generally larger (smaller) than at mid-depth and rotated slightly clockwise (counterclockwise). This may be inferred from the correlations between monthly anomalies of alongshore stress and current components off Cape Sable (Smith 1989b). At higher frequencies, the measured surface current responses to alongshore wind stress at C3 and C4 (not shown) fall within 25% of their low-frequency limits for periods down to 3 d, after which they decline sharply. This behaviour is consistent with the Greenberg model spinup time of less than 20 h (Wright et al. 1986). Thus the steady-state model gains may be reasonably used to estimate the wind-driven response in this region.

The forcing winds used to define the 2-D model current response were calculated from hourly winds recorded at Sable Island. The hourly observations were converted to sea surface wind stress using the formulae of Smith and Banke (1975), filtered using a Cartwright low-pass filter with 129 weights (cutoff frequency 0.036 cycles/h, 25% power passed at 28.4 h) and subsampled at 6-h intervals (see Lively (1984) for further

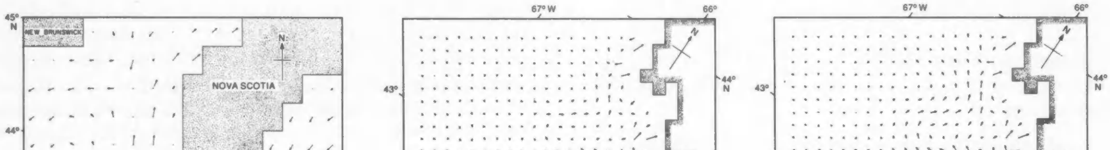


FIG. 2. Model velocity fields showing the Eulerian residual velocity vectors. (A) Lawrence and Trites (1983; $[V_{sum} + V_{win}]/2$), (B) Greenberg (1983) pure tidal residual, (C) Greenberg (1983) tidal residual + 4-cm set-up (exponential decay offshore) in coastal sea level on the eastern boundary of the full Greenberg grid at Halifax. (· specifies the origin of the vector).

details). Since the current gain decreases rapidly for periods below 3 d, we further smoothed the 6-h winds with an 11 point (66 h) running mean. This series was then linearly interpolated to half-hour intervals for input into the particle dispersion model.

Drogue Trajectories

In order to test the dispersion model, simulated particle trajectories are compared with the observed paths of satellite-tracked drogues. The drogue types, deployment times, locations, and trajectories have been described by Smith (1989a). During each deployment three to six drogues were released in a cluster and their positions recorded simultaneously 6–8 times a day by the ARGOS satellite system. For the present comparisons the time series of positions for each drogue were interpolated to hourly intervals. Tidal variations in position were removed by smoothing these series with a 13-h running mean. The centroid of the cluster was then calculated at hourly intervals.

Results

Model Check

As a check on the stability and accuracy of the numerical scheme, the particle-tracking model was tested against the analytical solution of Cheng et al. (1986) for the particular case of a Sverdrup wave propagating in the positive x-direction. Details of the simple case are given in the Appendix, including the correction of a small error in the formulas derived by Cheng et al. (1986).

The Sverdrup wave particle trajectories, calculated using a time step of 0.5 h and an iteration accuracy of 0.001 $m \cdot s^{-1}$, produced Lagrangian residual model displacements which differed from the analytical displacements by less than 3% after one and two tidal periods. The iteration accuracy was generally achieved with three or fewer iterations. Unless otherwise specified, we therefore used a 0.5-h time step and a 0.001 $m \cdot s^{-1}$ iteration accuracy for all model runs presented here.

Residual Circulation Patterns

The large-scale characteristics of the Lawrence and Trites (1983) and Greenberg (1983) Eulerian residual velocity fields are similar. The main features are clockwise gyres over Browns Bank, a westward flow between the western cap of Browns Bank and the coast of Nova Scotia and a strong eastward flow along the northeastern flank of Georges Bank. In the Lawrence and Trites (1983) residual field a single clockwise gyre surrounds the whole of Browns Bank, whereas the tidal residual field of the higher-resolution Greenberg (1983) model shows two smaller clockwise gyres over the Bank (Fig. 2a,b). To simulate Scotian Shelf inflow, the inclusion of the 4-cm coastal setup with an offshore exponential decay scale of 39 km on the eastern boundary of the Greenberg model enhances the magnitude of the westward flow into the Gulf of Maine, reduces the magnitude of the flow along the northern flank of Browns Bank, increases the cross-isobath component of this flow, increases the magnitude of the flow along the southern flank of the Bank and aligns this flow more closely with the isobaths (Fig. 2c). However, the flow on Georges Bank is not significantly affected. Henceforth the model flow field driven by nonlinear tidal interactions and the 4-cm coastal setup at Halifax will be referred to as the Greenberg residual circulation.

Comparison of Model and Observed Eulerian Residual Circulations

The Greenberg residual circulation is essentially the same as the one that Smith (1983) compared favourably with the observed depth-averaged annual-mean currents in the area. However, a comparison between model and observed near-surface Eulerian velocities at several mooring locations indicates that both models are underestimating the seasonal mean flow (Fig. 3). For this comparison the measured currents were averaged over the late-spring haddock spawning season (March, April, and May) using all available monthly mean data (Smith 1983, 1989a,b). At two locations (C4 and C7) the Lawrence and Trites (1983) and Greenberg velocities are similar and both underestimate the observed means by factors of three or four. At moorings C3 and C8 the Lawrence and Trites (1983) velocities exceed the Greenberg velocities by a factor of approximately three to five. The Lawrence and Trites (1983) velocities, in turn, underestimate the observed velocities by a factor of two to five.

On Browns Bank both models also underestimate observed mean Lagrangian velocities. The Greenberg residuals predict the time to circuit the western gyre of Browns Bank is approximately 40 d. This is four times greater than the 8–12 d indicated by the trajectories of satellite tracked drifters drogued between 5 and 15 m depth (Smith 1989a). The enhanced velocities of the Lawrence and Trites model do not fully account for this discrepancy.

Lagrangian Residual Circulation Pattern

To estimate the Lagrangian residual velocity field, the model particle trajectories from each grid point were calculated over one tidal cycle (12.5 h) and the displacement vectors to the end points were divided by the elapsed time. Not surprisingly, the Lagrangian velocities estimated from the Greenberg (1983) residuals alone (Fig. 4) are similar to the Eulerian velocities themselves (Fig. 2). When the tidal currents are included in the Eulerian field, the lowest order difference between the Lagrangian and Eulerian velocity is the Stokes drift ((u_{SD}, v_{SD}); see Appendix), plus a slight variation of the magnitude and direction of the Lagrangian current with the time of particle release (Fig. 5a) due to the second-order term in the Lagrangian residual current (the Lagrangian drift velocity (u_{LD}, v_{LD}); see Appendix, equations A.10 and A.12). In the nearshore region north of Browns Bank, the velocities may be deflected to the right or left of that estimated from the Eulerian residual only. On the southwestern flank of the Bank, bordering Northeast Channel, the off-bank component of the velocity is increased by the time-varying tidal flow, while on the northern flank nearest Cape Sable, the flow is opposite to that resulting from pure residual flow. The velocities along the eastern flanks of the Bank are relatively unchanged by the introduction of tidal currents. On the northern flank of Georges Bank, the Lagrangian velocity is in the same direction as the Eulerian velocity, but the average (over the tidal phase of release) magnitude is roughly two-thirds the Eulerian residual velocity, consistent with the theoretical expectations of Loder (1980). These differences are magnified in the comparison of 15-d particle trajectories (Fig. 5b).

Effect of Wind on the Circulation

The depth-averaged velocity fields generated by a 0.1 Pa wind stress (wind speed = 7 to 8 m/s) in the positive along-shore

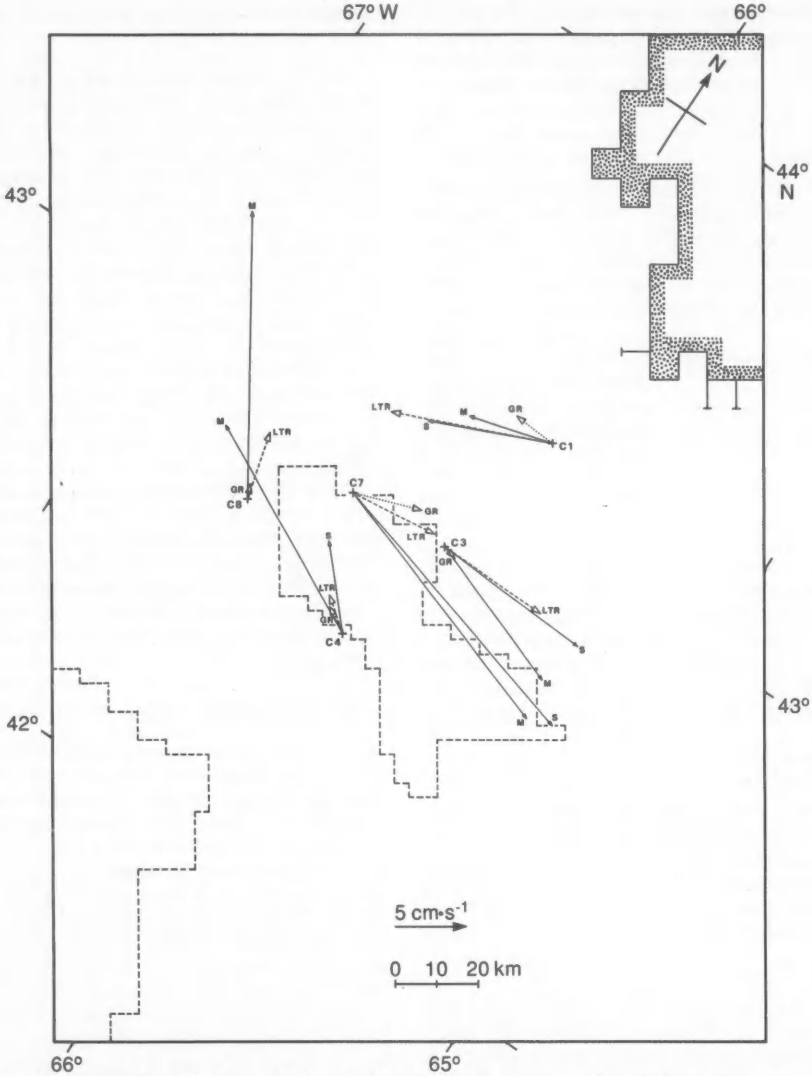


FIG. 3. A comparison of observed and model Eulerian mean current velocities. Observed currents are averaged over the haddock spawning months on Browns Bank (March, April, May). (+ specifies the origin of each vector; LTR, Lawrence and Trites residual; GR, Greenberg Residual; M, observed mid-depth velocity; S, observed near surface velocity; C1,C3,C4,C7,C8 are current meter locations).

and cross-shore directions are the same as those presented by Wright et al. (1986; their figures 4 and 5). The currents produced by the cross-shore stress are generally very weak and show little spatial variation. The along-shelf stress, on the other hand, produces relatively strong currents (order 0.05 m/s) throughout the Southwest Nova Scotia region. When these are added to the residual currents, the along-shelf wind-driven circulation is found to dominate the residual, whereas the cross-shelf wind has little effect in most of the region (Fig. 6). This is also reflected by the 4-d particle trajectories (Fig. 7a,b). In response to a steady along-shelf wind of 0.1 Pa, the particles move along an east–west axis at a rate of approximately 0.04 m/s, but cross-shelf winds produce very little net displacement of the particles.

These velocity fields and particle displacements are calculated using depth-mean currents which are most representative of the current pattern at mid-depth, i.e. away from the surface and bottom frictional layers. This level is appropriate for haddock larvae and perhaps the late-stage eggs. The earlier stage eggs, however, are concentrated within the surface Ekman layer. In the two-dimensional form of the equations, the Ekman transport ($\tau/\rho f$) is averaged over the depth (h) of the water column so that its contribution to the depth-averaged current is quite small, except in shallow (order 10 m) areas. A more realistic estimate of the effect of Ekman transport on the displacement of haddock eggs in the surface layer can be gained by subtracting the depth-mean Ekman transport from the total of wind-driven current plus residual, then adding back the velocity

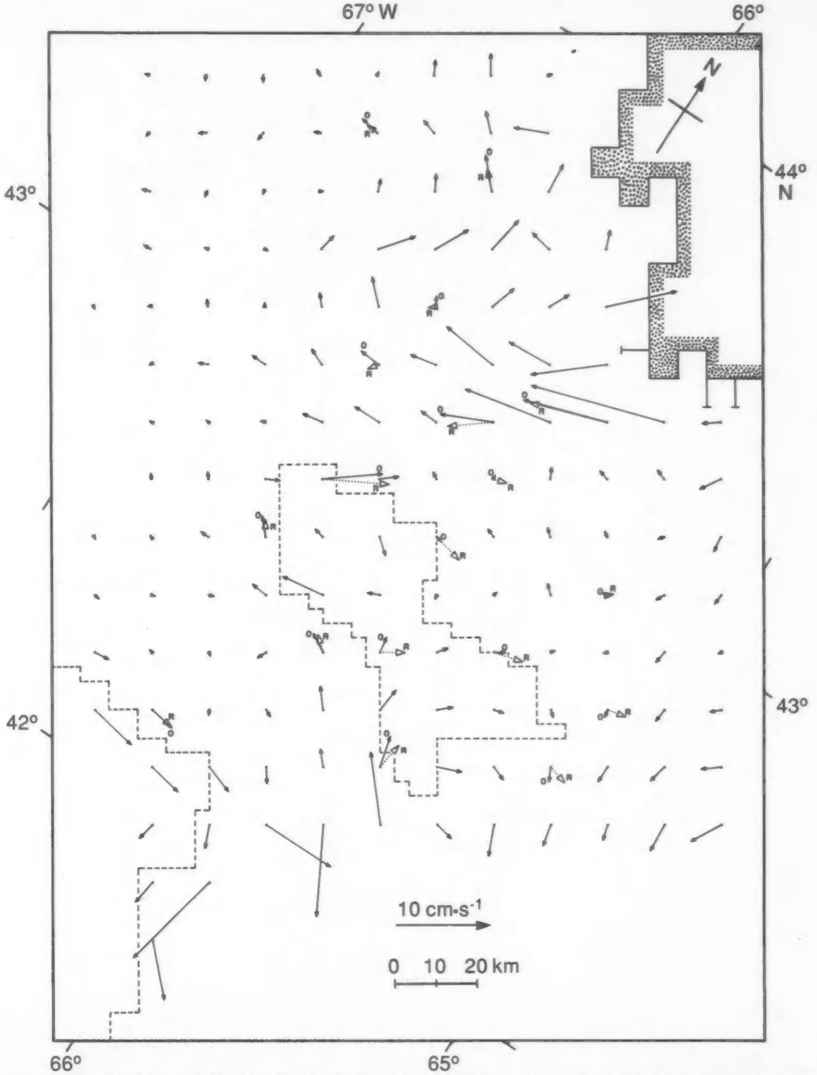


FIG. 4. Model velocity field showing the Lagrangian velocity vectors calculated after one tidal cycle using the Greenberg (1983) pure tidal residuals (dotted vectors) and tidal residuals + 4-cm coastal set-up at Halifax (solid vectors; see text). (+ specifies the origin of the vector; 0 specifies the particle was released at $t_o = 0$)

obtained by distributing the Ekman transport over the depth of the surface Ekman layer, assumed to be 30 m (based on scaling estimates for a 0.1 Pa wind stress and observed mixed-layer depths in spring). The enhanced surface velocity fields are shown in Fig. 8a–d. The current field associated with the alongshelf wind is much the same as with depth-averaged Ekman transport, although the velocities are now somewhat greater. On the other hand, the surface circulation associated with the cross-shelf stress is greatly increased and consists primarily of a uniform Ekman-dominated current approximately 0.05 m/s. By comparison with Fig. 2c, it is clear that the surface-enhanced components of a circulation driven by 0.1 Pa stresses dominate the pure residual flow, although for cross-shelf wind, a weak gyre still exists over the western cap of Browns Bank (Fig. 8c,d). In all of these cases, the southwestward along-shelf wind (opposite to that in Fig. 9a) causes the gyre on the western cap of Browns Bank to open, such that particles can escape from the Bank in a northerly direction. An offshore wind allows some particles to escape toward the west (Fig. 9b).

The question now arises as to whether steady or time-dependent stresses are more effective in controlling particle trajectories in the surface layer. The mean alongshore stresses at Yarmouth and Sable Island are small (order 0.01 and 0.02 Pa, respectively) and correspond to currents of only 0.003 m/s (Smith 1989b). Variable stresses, on the other hand, have amplitudes of order 0.1 Pa for periods less than 1 mo (0.08 and 0.13 Pa for periods of 10–30 d and 2–10 d, respectively; Smith 1989a), and therefore drive significant currents on the biolog-

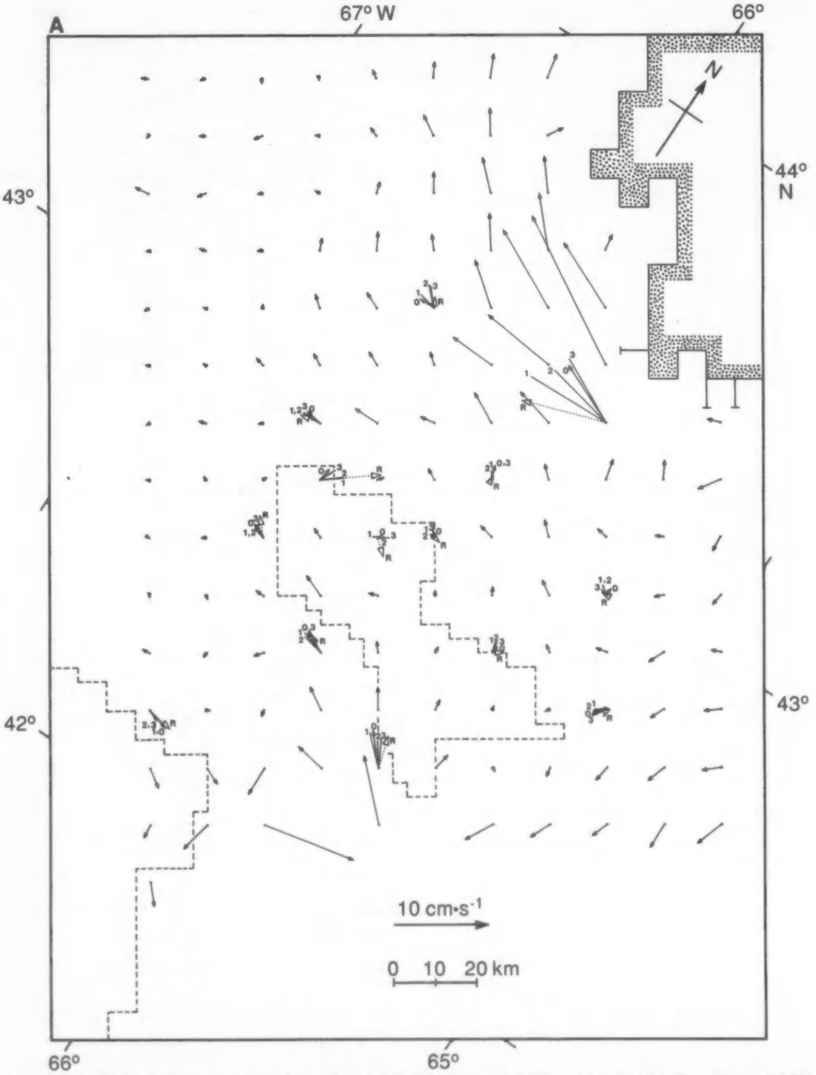


FIG. 5. (A) Model Lagrangian velocity field calculated after one tidal cycle using the Greenberg (1983) tidal residuals + 4-cm coastal set-up (dashed, '*R*' at top) and the tidal residuals + 4-cm coastal set-up + tidal currents (solid). The complete field of solid vectors represents Lagrangian velocities for particles released at $t_o = 0$. At selected grid points, numbers shown at the tips of the four solid vectors

ical time scales of interest. In order to investigate further the influence of the wind-driven currents, the particle trajectories were calculated using a periodic wind stress with an amplitude of 0.1 and 0.4 Pa and a period of 8 d. The 8-d trajectories of single particles released at several locations were estimated using (1) residual + tidal currents and (2) wind + residual + tidal currents. Figure 10a,b shows that the 0.1 Pa oscillatory wind has little effect on the net particle displacements. This result also applies to the stronger wind stress forcing (0.4 Pa; results not shown).

Drogue Trajectories

In order to evaluate the model's ability to reproduce the trajectories of passively drifting particles in the surface layer, hypothetical particles were introduced into the model flow fields at the co-ordinates corresponding to the centroid of a cluster of satellite-tracked drifters drogued at 10 m. We chose four drogued–drifter trials for comparison: April and November 1983, May 1984, and May 1985.

During April of 1983, drifters were released over the western cap of Browns Bank, in the eastern half of the cap gyre, and quickly drifted off the Bank in a northerly direction. Smith (1989a) suggested this was due to the westward wind component prevailing throughout the deployment period. The simulated trajectory, using the Greenberg residual flow plus surface-enhanced wind drift (Fig. 11a) qualitatively reproduces the observed trajectories, but underestimates the net displacement

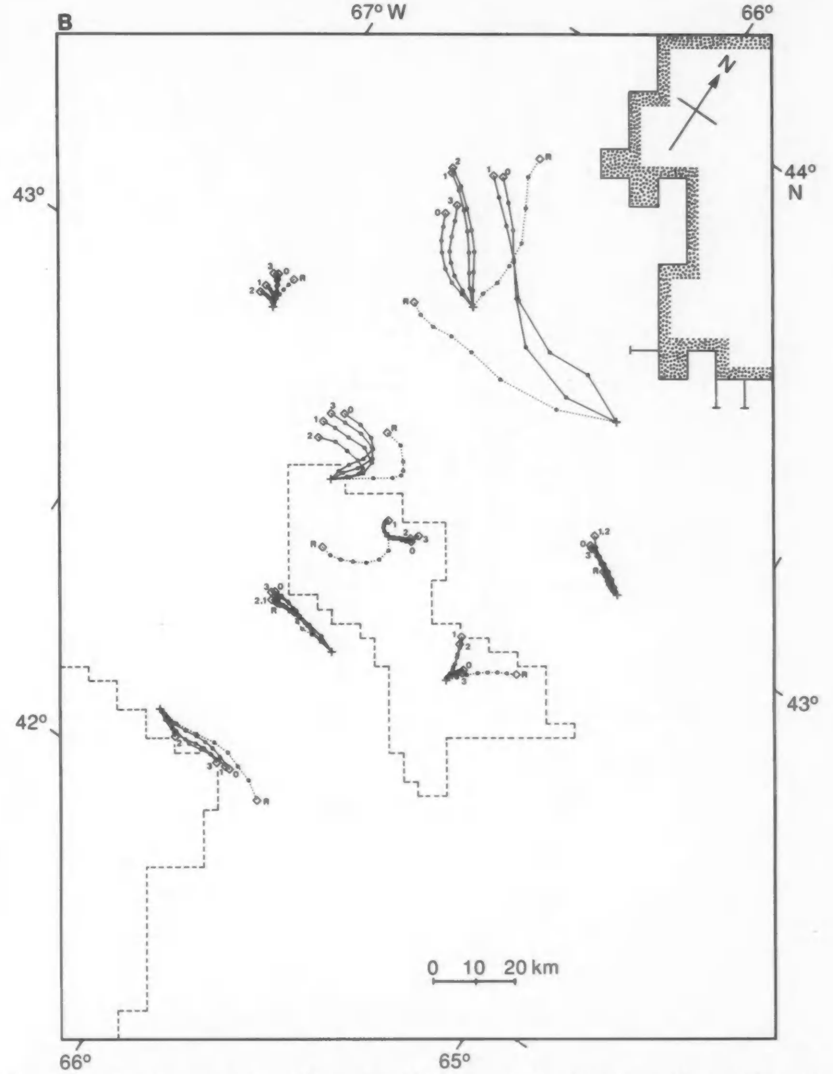


FIG. 5. *(continued)* correspond to different times (tidal phases) of particle release (0, $t_o=0$; 1, $t_o=T/4$; 2, $t_o=T/2$; 3, $t_o= 3T/4$; $T = 2\pi/\omega$ = tidal period). (B) 14.5-d (28 tidal cycles) particle trajectories. The solid and dashed lines refer to trajectories calculated using the Eulerian currents as specified in Fig. 5a. (+ specifies the origin of each vector or trajectory; diamonds specify the end position of a trajectory; large dot marks the end of every fourth tidal cycle).

by roughly a factor of four. This comparison also shows the danger in using the residual circulation as the sole estimate of the circulation. The particle trajectory estimated from the residual circulation alone is toward the east in compliance with the western cap gyre and toward the northwest when the tidal currents are included. Inclusion of the wind accelerates the displacement in this latter direction.

A similar conclusion is reached by comparing observed and simulated particle tracks in November 1983 (Fig. 11b). Drogues were released on the northwest peak of the Bank at the start of two consecutive periods and recovered after drifting for approximately 2d. During the first period, the prevailing wind was from the east (easterly) and the drogues were displaced to the northwest. The model tracks also show this but underestimate the displacement by nearly a factor of five. At the start of the second period, the prevailing wind was westerly and the drogues were displaced to the southwest. The model track (with wind) shows this tendency also, but some of the effect is lost because of the smoothing of the wind field for the model calculation. Clearly, though, the model displacements are smaller than observed for this trial as well.

The third and fourth drifter trials were conducted in almost identical positions on the eastern flank of Browns Bank; one cluster released in May 1984 and the other in May 1985. In 1984 the drogues drifted rapidly toward the west, skirted the perimeter of the western cap gyre and exited the Bank from its

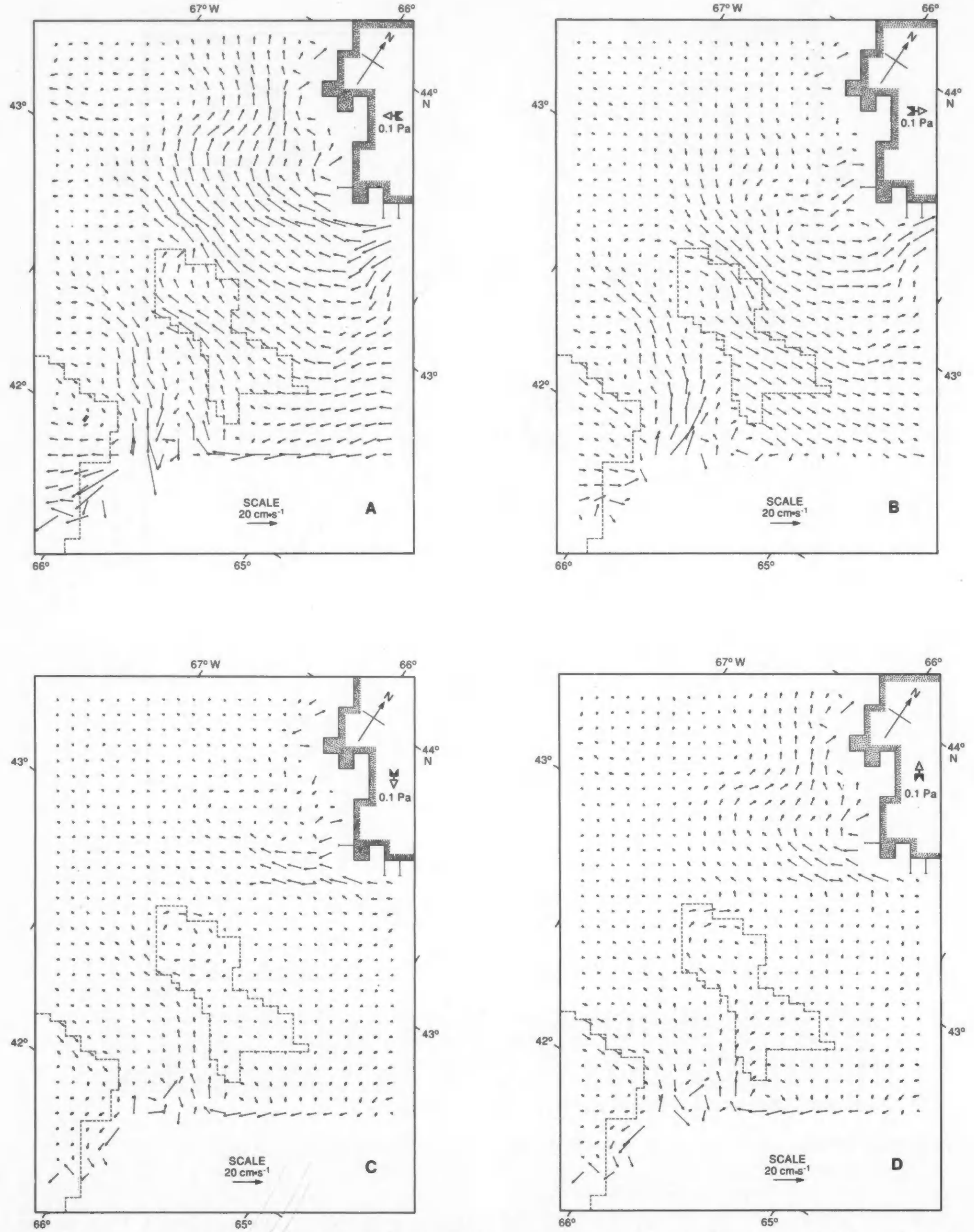

67° W
66°
43°
44° N
0.1 Pa
42°
43°
SCALE
20 cm·s⁻¹
A
66°
65°
67° W
66°
43°
44° N
0.1 Pa
42°
43°
SCALE
20 cm·s⁻¹
B
66°
65°
67° W
66°
43°
44° N
0.1 Pa
42°
43°
SCALE
20 cm·s⁻¹
C
66°
65°
67° W
66°
43°
44° N
0.1 Pa
42°
43°
SCALE
20 cm·s⁻¹
D
66°
65°

FIG. 6. Model Eulerian velocity field including pure tidal residual, 4-cm coastal set-up on eastern boundary at Halifax and depth-averaged response to 0.1 Pa wind stress. (a) $-\tau_y$, alongshelf, (b) $+\tau_y$, (c) $+\tau_x$, cross-shelf, (d) $-\tau_x$. (· specifies the origin of each vector).

northern flank (Fig. 11a). In 1985 the drogues drifted slowly in the opposite direction, toward the east (Fig. 11b). The model cannot reproduce these trajectories. The pure residual and residual plus tidal circulations produce slow trajectories toward the east. When the wind is included, the 1984 model trajectory is toward the east, in the opposite direction to the observed displacements. In 1985 the wind was weak and produced no significant current.

The drogue trajectories were also simulated using the Lawrence and Trites (1983) residual flow field plus 3% of the smoothed wind speed (66 h running mean), an approach used by Lawrence and Trites and commonly used in oil spill models.

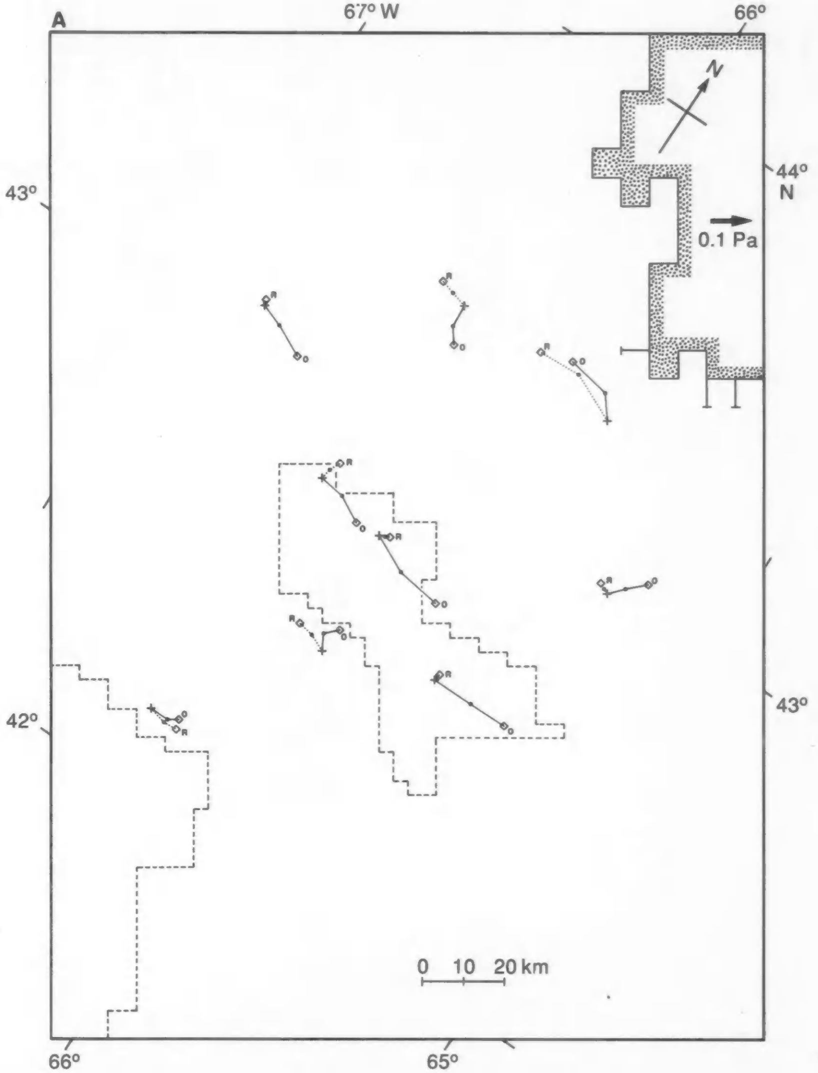

A
67° W
66°
N
44°
N
0.1 Pa
43°
R
O
42°
43°
0 10 20 km
66°
65°

FIG. 7. (A) Particle trajectories, 4.2-d (eight tidal cycles), calculated using Greenberg pure tidal residuals + 4-cm coastal set-up at Halifax + tidal currents ($t_o = 0$) + depth-averaged responses to constant 0.1 Pa alongshelf wind stress. (B) cross-shelf wind stress. The solid (dashed) lines refer to trajectories

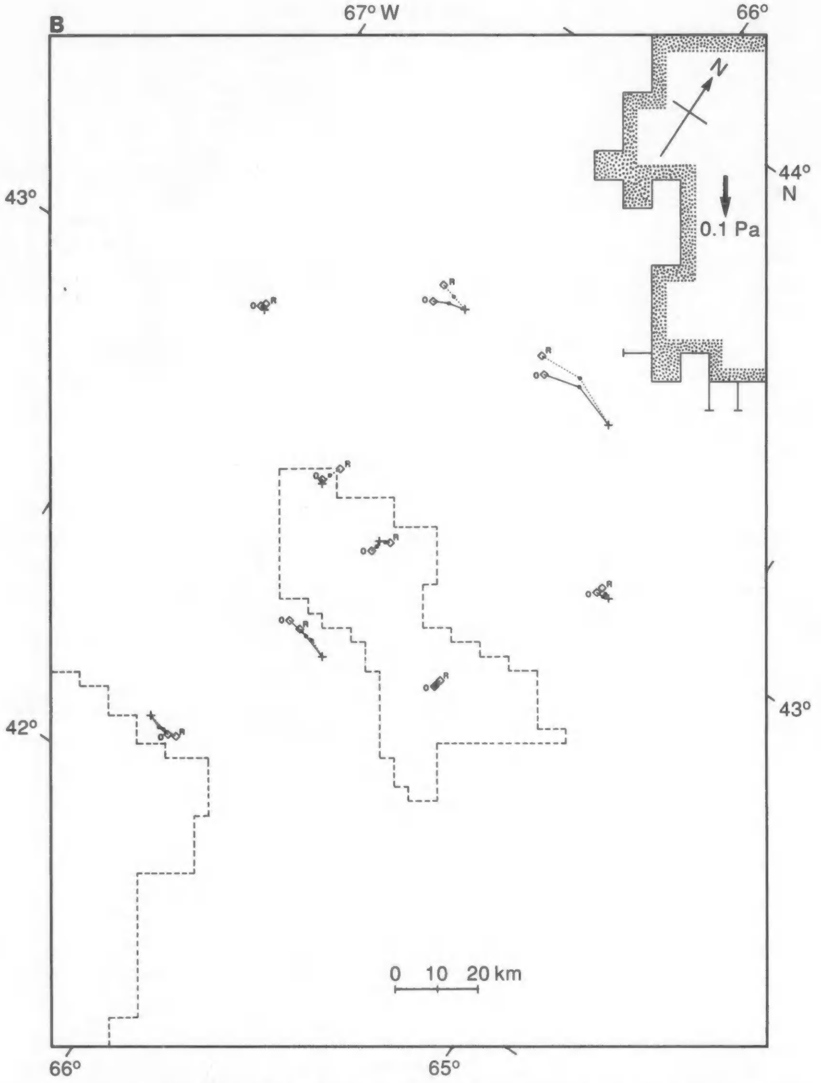
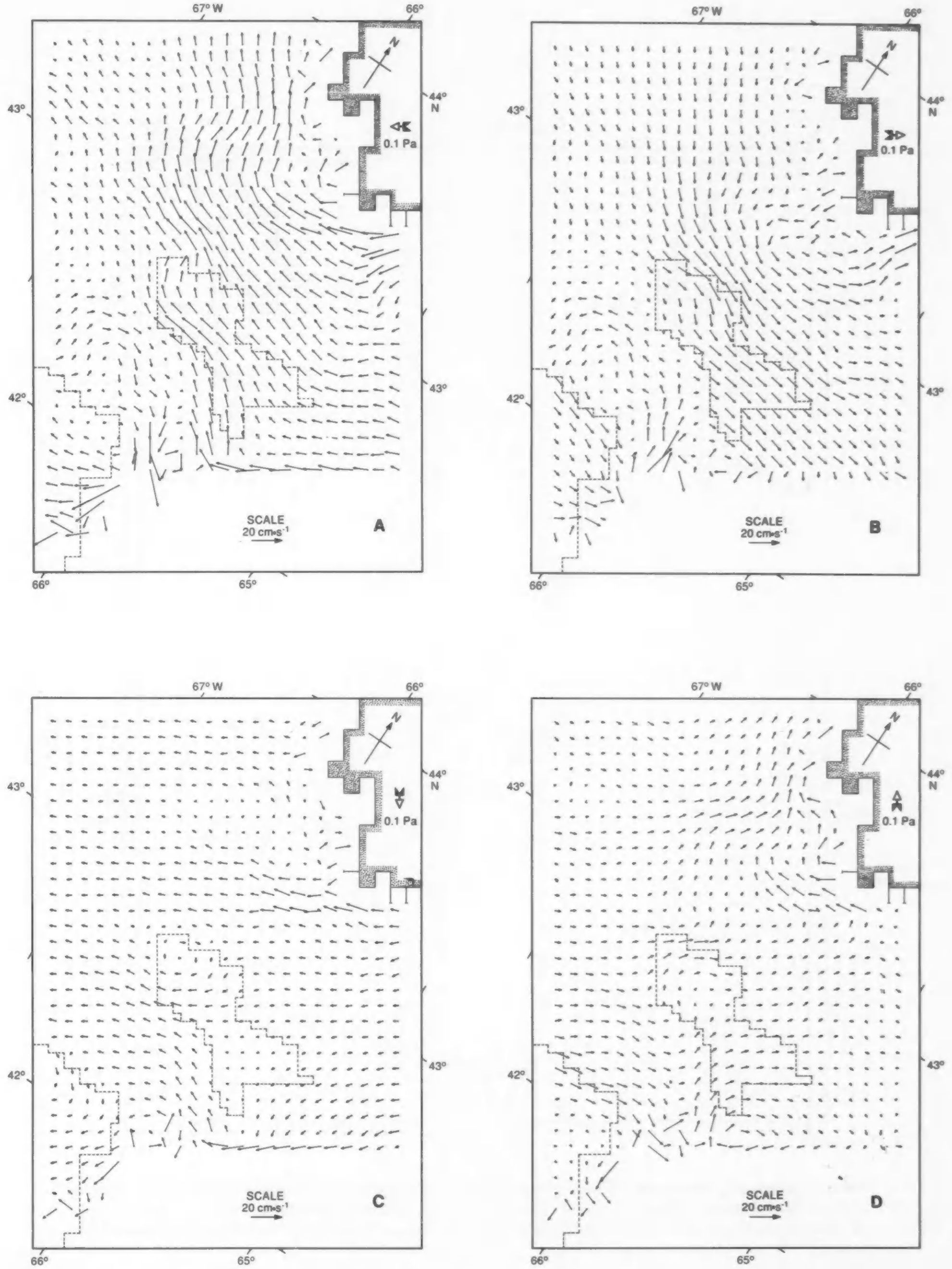

B
67° W
66°
44° N
43°
0.1 Pa
N
42°
43°
0 10 20 km
66°
65°
R

FIG. 7. (*continued*) calculated with (without) a wind-driven component. (+ specifies the origin of each trajectory; diamonds specify the end position of a trajectory; large dot marks the end of every fourth tidal cycle).


67° W
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0.1 Pa
SCALE
20 cm•s⁻¹
A
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44° N
43°
42°
43°
0.1 Pa
SCALE
20 cm•s⁻¹
B
66°
65°
67° W
66°
44° N
43°
42°
43°
0.1 Pa
SCALE
20 cm•s⁻¹
C
66°
65°
67° W
66°
44° N
43°
42°
43°
0.1 Pa
SCALE
20 cm•s⁻¹
D
66°
65°

FIG. 8. Model Eulerian velocity including pure tidal residual, 4-cm coastal setup at Halifax, and surface-enhanced responses to 0.1 Pa wind stresses (see text) (A) $-\tau_y$, alongshelf, (B) $+\tau_y$, (C) $+\tau_x$, cross-shelf, (D) $-\tau_x$. (· specifies the origin of each vector).

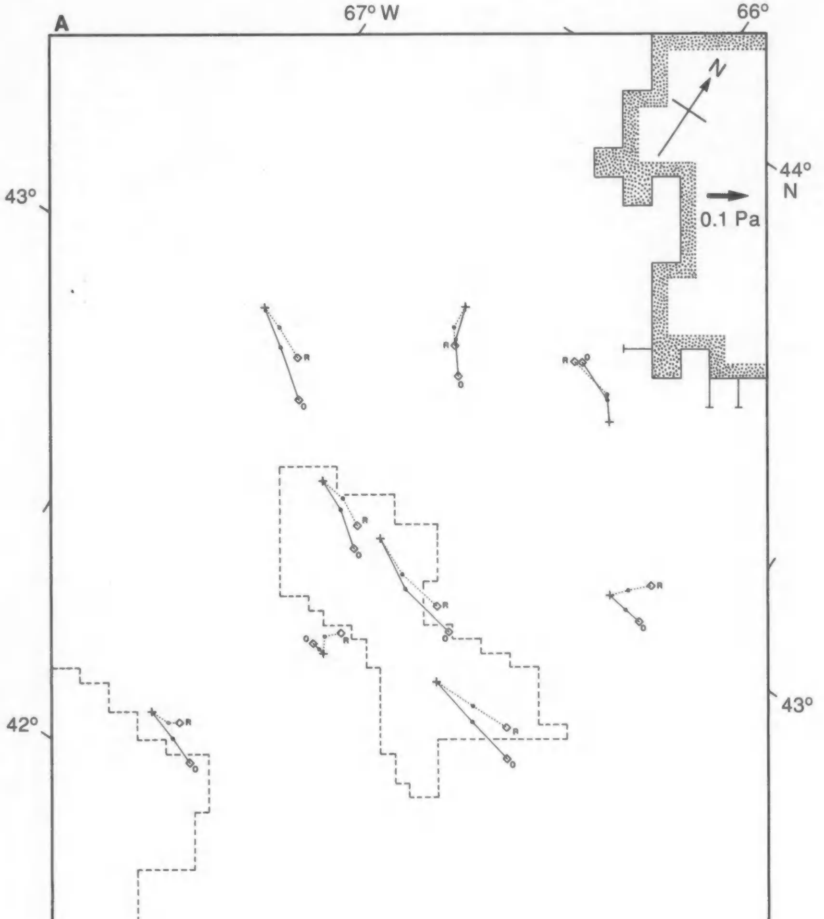
A
67° W
66°
44° N
0.1 Pa
N
43°
43°
42°
66°
65°
R
O
0 10 20 km

FIG. 9. (Particle trajectories, 4.2-d (eight tidal cycles), calculated using Greenberg pure tidal residuals + 4-cm coastal set-up at Halifax + tidal currents ($t_o = 0$) + surface-enhanced responses to constant 0.1 Pa alongshelf (A) and cross-shelf (B) wind stresses. The solid (dashed) lines refer to trajectories

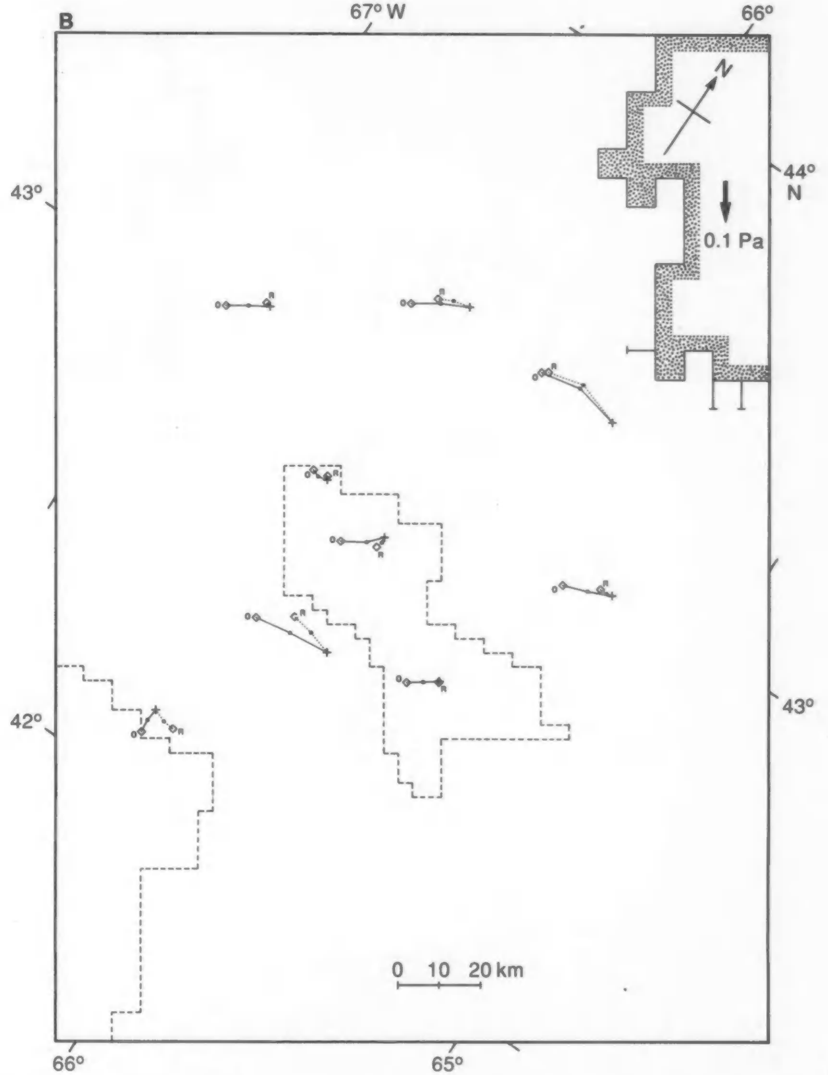
B
67° W
66°
43°
44° N
0.1 Pa
N
42°
43°
0 10 20 km
66°
65°
R

FIG. 9. *(continued)* calculated with a surface-enhanced (depth-averaged) wind-driven components. (+ specifies the origin of each trajectory; diamonds specify the end position of a trajectory; large dot marks the end of every fourth tidal cycle).

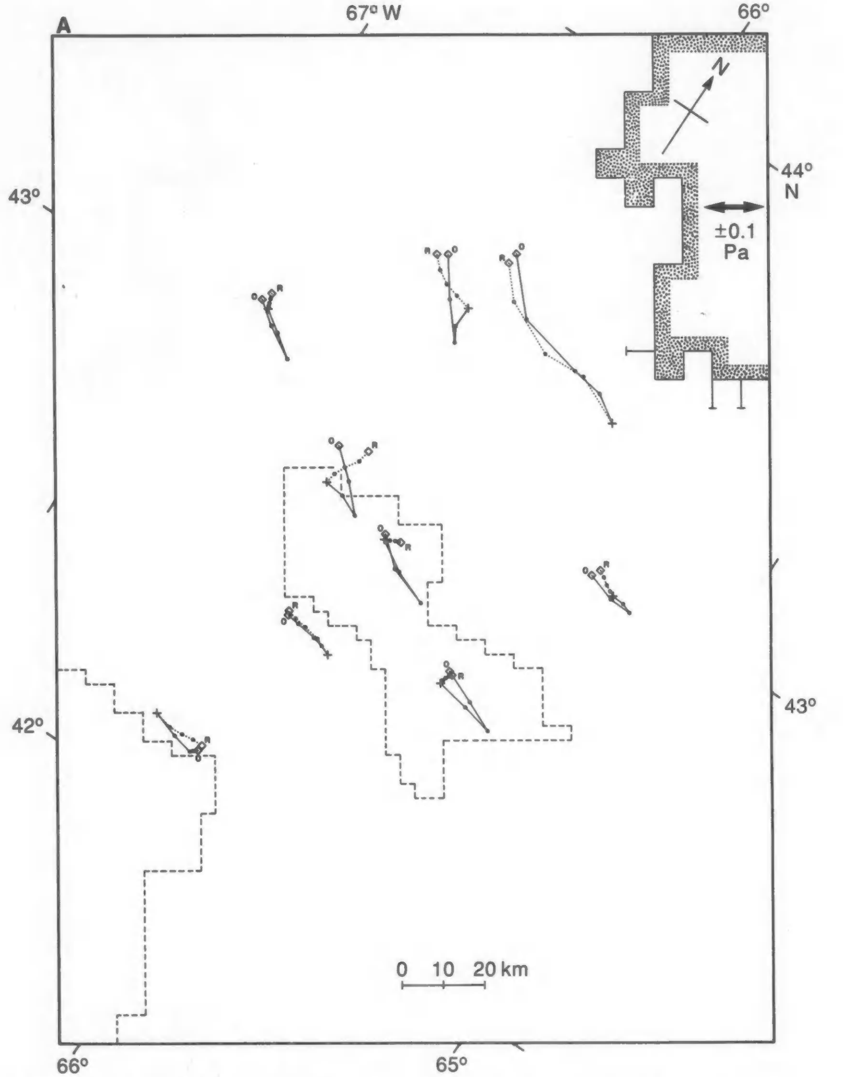
A
67° W
66°
44° N
±0.1 Pa
43°
42°
43°
0 10 20 km
66°
65°

FIG. 10. Particle trajectories, 8.3-d (16 tidal cycles), calculated using Greenberg pure tidal residuals + 4-cm coastal set-up at Halifax + tidal currents ($t_o = 0$) + surface-enhanced responses to 0.1 Pa periodic [$0.1 \sin(2\pi t/P)$, P = 16 tidal cycles] alongshelf (A) and cross-shelf (B) wind stresses. The

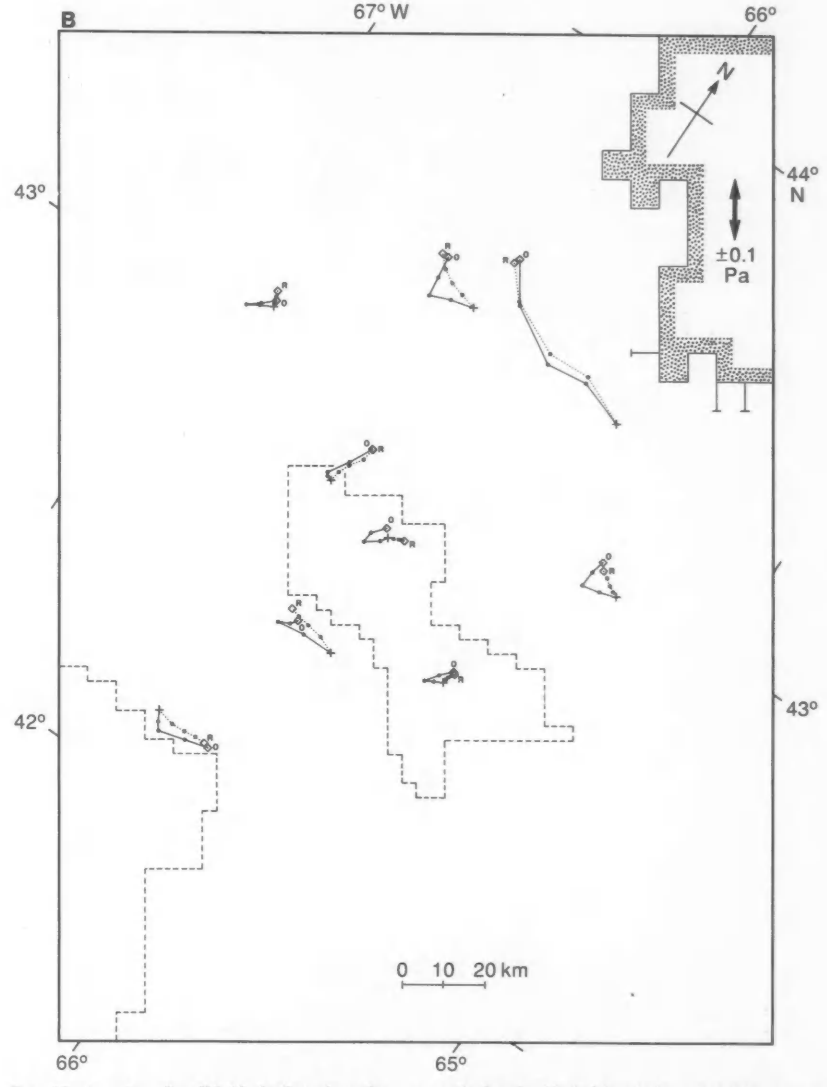
B
67° W
66°
N
44°
N
±0.1
Pa
43°
R
O
43°
42°
0 10 20 km
66°
65°

FIG. 10. *(continued)* solid (dashed) trajectories were calculated with (without) the wind-driven components of the circulation. (+ specifies the origin of each trajectory; diamonds specify the end position of a trajectory; large dot marks the end of every fourth tidal cycle).

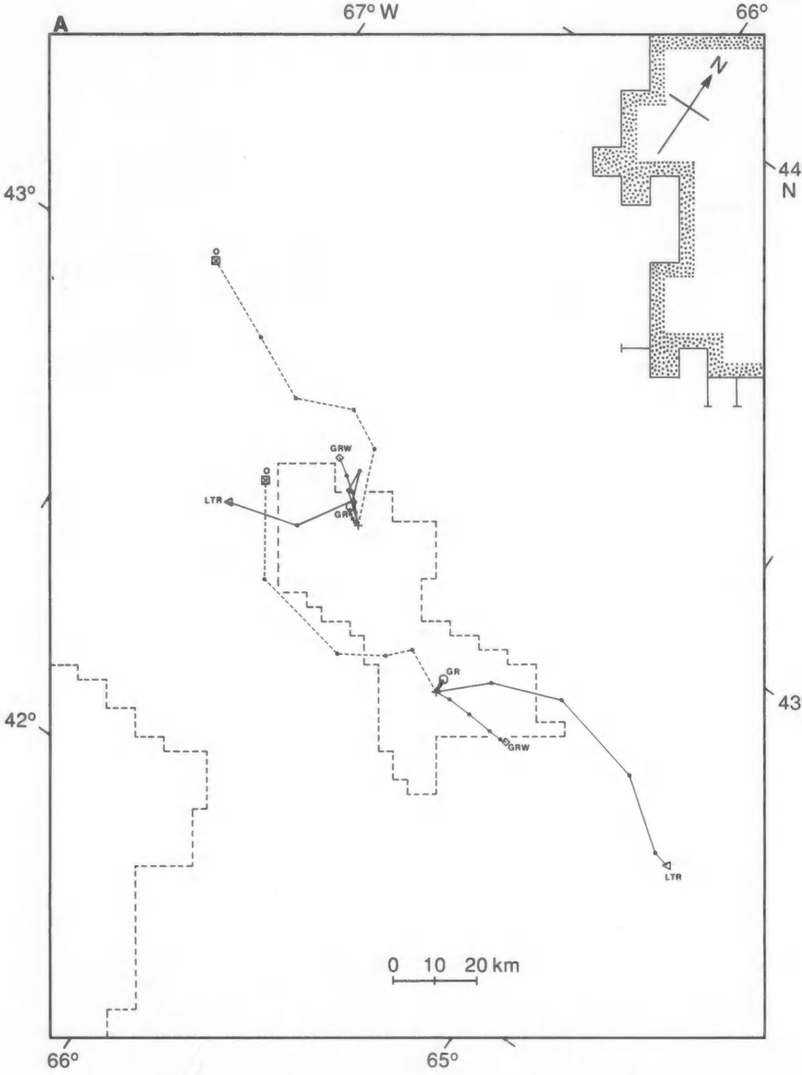
A
67° W
66°
N
44°
N
43°
o
GRW
o
LTR
GR
GR
43°
42°
GRW
LTR
0 10 20 km
66°
65°

FIG. 11. A comparison between observed and simulated drogue trajectories. (A) northwest quadrant Browns Bank; April 1983, southeast quadrant Browns Bank; May 1984, (B) northwest quadrant Browns Bank; November 1983, southeast quadrant Browns Bank; May 1985. (GR, Greenberg residual only;

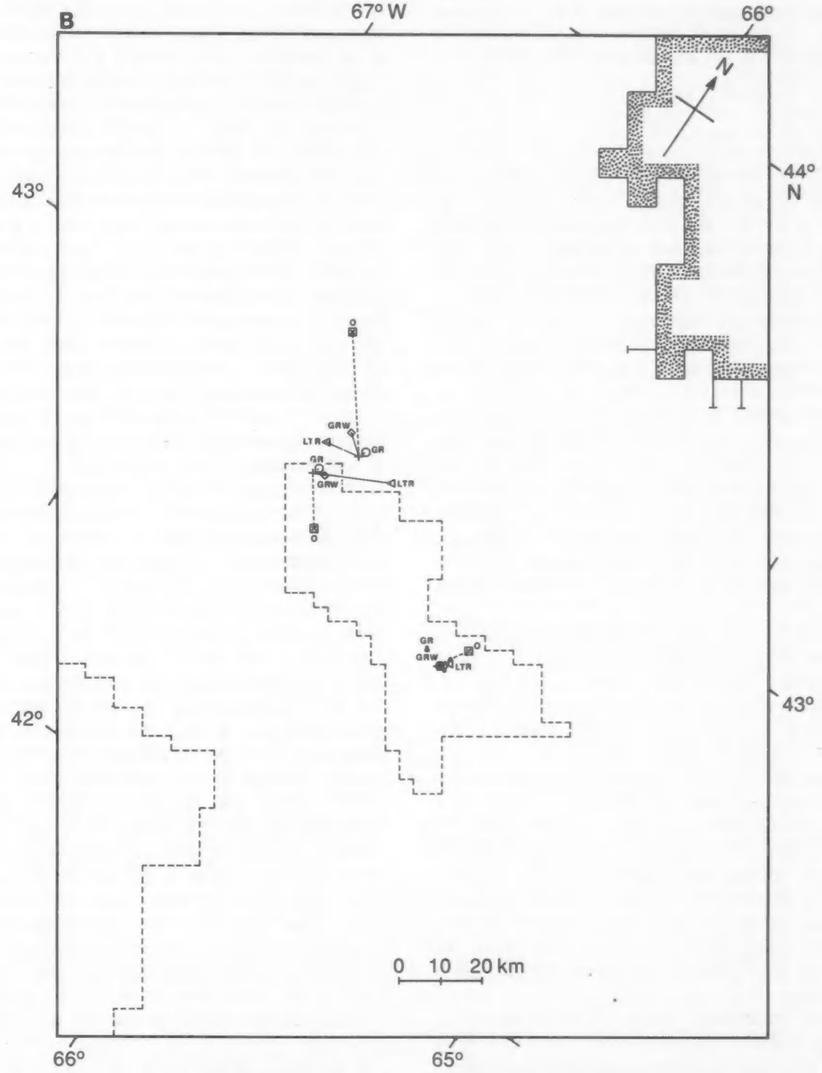
B
67° W
66°
N
44°
N
43°
43°
42°
GRW
LTR
GR
O
GR
GRW
LTR
O
GR
&
GRW
O
LTR
0 10 20 km
66°
65°

FIG. 11. (*continued*) GRW, Greenberg residual + surface enhanced wind driven current; LTR, Lawrence and Trites residual + 3% of the wind speed; O, Observed drogue trajectory; + specifies the origin of each trajectory; open symbols specify the end position of a trajectory; large dot marks the end of every fourth tidal cycle).

Although the simulated displacements generally exceeded those produced using the Greenberg model, the displacements still underestimated the observed trajectories. The directions of the Lawrence and Trites based trajectories are not as close to the observed directions as are the Greenberg-based simulations. This is probably due to the fact that the 3% of the wind speed estimation of the wind response does not account for topographic steering of the wind driven flow. This effect is particularly evident in the April 1983 simulations in which the wind drives the drogues off the Bank toward the northwest in the Greenberg simulations and toward the southwest in the Lawrence and Trites simulations.

Discussion

In pursuit of our long-term goal to develop an ichthyoplankton dispersion model for the Southwest Nova Scotia region, our first step has been to evaluate the adequacy of some available circulation models. Existing empirical descriptions of the mean Lagrangian (Bumpus and Lauzier 1973; Harding and Trites 1988) and pseudo-Lagrangian (Lawrence and Trites 1983) circulations are of low spatial resolution and are not readily adapted to include time-varying circulations. Since the Eulerian circulation in the Southwest Nova Scotia area is dominated by M_2 tidal and wind-driven components (Smith 1983, 1989a), we have focused on the high-resolution (ca. 7 km grid squares), depth-averaged tidal, and wind-driven models of Greenberg (1983) and Wright et al. (1986). In spite of known discrepancies between the model residual circulation and observations, we have pursued the analysis in order to (1) test the hypothesis that the dominant components of the Eulerian circulation control the Lagrangian displacement fields, (2) investigate the sensitivity of Lagrangian drift, and (3) provide a framework for future studies.

The spatial variation in tidal amplitudes and phases gives rise to Lagrangian mean velocities which differ from the Eulerian means. The magnitude of this difference varies spatially, with greatest differences found on the northern flank of the western cap of Browns Bank. In this region, where Smith (1989a) observed most of his satellite drifters to exit the Bank, the Lagrangian velocities are generally deflected northward toward Cape Sable and, during particular phases of the tide, are opposite in direction to the Eulerian currents. Physically, particles released at various stages of the tide are injected into different water columns whose average displacements over the tidal cycle are not the same. The differences in displacement are most acute on the northern flank because of the sharp changes in the tidal currents and strong mean shears. In most other areas the Lagrangian velocities are similar in magnitude and direction to the Eulerian velocities.

For persistent moderate wind stresses (0.1 Pa), the wind-driven currents may dominate the residual flow field and therefore have a strong influence on the model particle trajectories. This is particularly true of alongshelf winds which produce strong pressure gradients as well as a surface Ekman layer to drive the current, whereas cross-shelf winds produce only a significant surface Ekman flow. Using rough estimates of the average wind-driven response in the surface layer, Smith (1989a) showed that the winds alone in April and November 1983, were sufficient to "kick" the satellite drogues off the Bank to the north, though the observed displacements were underestimated. He felt that a more accurate description of the tidal and residual circulations would produce quantitative agreement.

However, the model computations have shown that the net displacements caused by oscillatory winds of realistic amplitude are small, and hence the accurate specification of the residual circulation appears to be crucial for simulating the displacement fields over the biological time scales of interest. When forced with real winds and tides, the model does not accurately reproduce the trajectories of satellite-tracked drifters, particularly over the eastern half of Browns Bank. Over the western cap the simulated trajectories are qualitatively, but not quantitatively, similar to the observed trajectories. As Smith (1989a) suggested, the "leakiness" of the western cap gyre is partly due to wind-driven currents, but the model indicates that the mean longshore pressure gradient (associated with the 4-cm residual setup at Halifax) and the tidal currents are also important components driving this off-bank Lagrangian flow. However, the model underestimates the observed displacements, probably as a result of underestimation of the magnitude of the seasonal residual circulation by a factor of two to five (Fig. 3). Part of this discrepancy is due to the fact the Greenberg (1983) model does not adequately resolve the bottom topography and therefore underestimates the tidally-rectified current (Tee et al. (1987), but a significant portion of the difference between model and observation might also be due to the presence of strong unmodelled baroclinic currents. The seasonal supplies of fresh coastal water in the Nova Scotian Current and warm, salty slope water in Northeast Channel give rise to strong horizontal and vertical density gradients that support baroclinic currents on the order of 0.10 $m \cdot s^{-1}$ (Smith 1983; 1989a).

On the eastern half of Browns Bank the model does not simulate the drogue trajectories either qualitatively or quantitatively. Furthermore, comparison of the drogue tracks from May 1984 and 1985 indicates a distinct component of interannual variability. Rather than seasonal density variations, these differences may be associated with the presence of Gulf Stream rings in the slope water to the south. Rings were observed in satellite infrared images south of Browns Bank in both 1984 and 1985, during the period of the drogue releases. In 1984, a surface streamer of modified ring water extended shoreward along the eastern edge of Northeast Channel, but in 1985 there was no evidence for the active intrusion of slope water. The 1984 event may have caused the large difference in the drogue trajectories for that year versus 1985 (Fig. 11).

Although model and drogue trajectories were not compared in the nearshore region to the north of Browns Bank, the reasonable agreement between model and observed residual currents in this area (Fig. 3) suggests that the model particle trajectories may have some reality. However, long-term current meter records suggest that the nearshore circulation off Cape Sable varies considerably on time scales of a month and longer. In particular, the annual cycles of the alongshore currents have amplitudes in the range of 0.04 and 0.06 m/s (i.e. comparable with the annual mean), while interannual variations that are not accounted for by the wind also measure 0.04 $m \cdot s^{-1}$ (Smith 1989b). Thus even if the annual cycle and wind-driven components of the circulation are modelled, a significant unknown component remains. It too is probably related to baroclinic forcing (Smith 1983).

The question of how useful this model would be for assessing interannual variability of egg dispersion, and subsequent comparisons with year-class sizes for a particular Browns Bank fish stock is difficult to answer, since the accuracy of the predicted displacements of ichthyoplankton would depend on the strength of the variable winds, the time of spawning relative to the seasonal cycle in the circulation, the degree to which the real low-frequency circulation deviates from the model residual, and the spatial distribution of the spawning adults. If there were strong interannual signals in the alongshore component of windstress and if the important spawning sites were located on or about the western cap of Browns Bank, then an index based on the model response to wind might give a good indication of the fate of positively buoyant eggs and larvae. However, comparison of the model trajectories against drogue tracks suggests that such an index would be qualitative at best. On the other hand, if most of the spawning were located over the southeastern part of the Bank, the model might give a very poor representation of the true distribution. Ichthyoplankton surveys indicate major spawning activity occurs over both the western and eastern portions of the Bank (Koslow et al. 1985). Obviously, the model cannot now be applied confidently without some means of testing the outcome, or at least validating the model circulation and spawning distribution in the time period of interest.

Although the Greenberg-based model appears to give trajectories that are qualitatively more representative of the observed trajectories than are the Lawrence-and-Trites-based trajectories, particularly with respect to direction over the western cap of Browns Bank, substantial improvements in the capabilities of this and similar models requires some means of monitoring and incorporating baroclinic components of the circulation. Time series of satellite infrared imagery will be of some use. However, since these are not always good indicators of the circulation (Smith 1989b) some sort of in situ measurements at strategic locations may be required. Another important step would be to improve the spatial resolution of the model in order to reflect the observed tidally-induced circulation more accurately, particularly on the northern flank of the Bank.

Acknowledgements

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References

Abramowitz, M., and I. Stegun. 1964. Handbook of mathematical functions, applied mathematical series, Vol. 55 (Washington National Bureau of Standards)

Bailey, K. M. 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Mar. Ecol. Prog. Ser. 6: 1–9.

Bartsch, J. 1988. Numerical simulation of the advection of vertically migrating herring larvae in the North Sea. Meeresforsch. 32: 30–45.

Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bur. Fish. 40(2): 1–509.

1927. Physical oceanography of the Gulf of Maine. Bull. U.S. Bur. Fish. 40(2): 1027 p.

Bumpus, D. F., and L. M. Lauzier. 1965. Surface circulation on the continental shelf of eastern North America between Newfoundland and Florida. Serial atlas of the marine environment. Am. Geogr. Soc., New York, N.Y.

Carruthers, J. N., A. L. Lawford, and V. F. C. Veley. 1951a. Fishery hydrography: brood-strength fluctuations in various North Sea fish, with suggested methods of prediction. Kieler Meeresforschungen 8: 5–15.

Carruthers, J. N., A. L. Lawford, V. F. C. Veley, and B. B. Parrish. 1951b. Variations in brood-strength in the North Sea haddock, in light of relevant wind conditions. Nature (Lond.) 168: 317–319.

Chase, J. 1955. Winds and temperature in relation to the brood-strength of Georges Bank Haddock. J. Cons. Perm. Int. Explor. Mer 21: 17–24.

Cheng, R. T., S. Feng, and P. Xi. 1986. On Lagrangian residual ellipse, p. 102–113. *In* J. van de Kreefe [ed.] Lecture notes on coastal and estuarine studies — physics of shallow estuaries and bays. Springer-Verlag, New York, NY.

Colton, Jr., J. B. 1965. The distribution and behaviour of pelagic and early demersal stages of haddock in relation to sampling techniques. ICNAF Spec. Publ. 6: 317–333.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, London, England. 278 p.

1981. Fisheries biology. 2nd ed. University of Wisconsin Press, Madison, WI. 295 p.

Day, C. G. 1958. Surface circulation in the Gulf of Maine as deduced from drift bottles. U.S. Fish and Wildl. Serv., Fish. Bull. 141: 443–472.

Forrester, C. K. 1973. A method of time centering the Lagrangian marker particle computation. J. Comput. Physics 12: 269–274.

Greenberg, D. A. 1983. Modelling the mean barotropic circulation in the Bay of Fundy and Gulf of Maine. J. Phys. Oceanogr. 13: 886–904.

Harden-Jones, F. A. 1965. Fish migration and water currents, ICNAF Spec. Publ. No. 6: 257–266.

1968. Fish migration. Edward Arnold, London, England. 325 p.

Harding, G. C., and R. W. Trites. 1988. Dispersal of *Hommarus americanus* larvae in the Gulf of Maine from Browns Bank. Can. J. Fish. Aquat. Sci. 45: 416–425.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe. Rapp. P-V. Reun. Cons. Int. Explor. Mer 20: 1–13.

Hunter, J. R. 1987. The application of Lagrangian particle-tracking techniques to modelling of dispersion in the sea, p. 257–269. *In* J. Noye [ed.] "Numerical modelling: applications to marine systems." Elsevier Science Publishers B.V. (North-Holland).

Iles, T. D., and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science (Wash., DC) 215: 627–633.

Isaji, T., and M. L. Spaulding. 1984. A model of the tidally induced residual circulation in the Gulf of Maine and Georges Bank. J. Phys. Oceanogr. 14: 1119–1126.

Koeller, P. A., P. C. F. Hurley, P. Perley, and J. D. Neilson. 1986. Juvenile fish surveys on the Scotian Shelf: implications for year-class size assessments. J. Cons. Int. Explor. Mer 43: 59–76.

Koslow, T., S. Brault, J. Dugas, and F. Page. 1985. Anatomy of an apparent year-class failure: the early life history of the 1983 Browns Bank haddock (*Melanogrammus aeglefinus*) Trans. Am. Fish. Soc. 114: 478–489.

Lawrence, D. J., and R. W. Trites. 1983. Surface oil spill trajectory modelling for Georges and Browns Banks. Can. Tech. Rep. Hydrogr. Ocean Sci. 29: 16 p.

Loder, J. W. 1980. Topographic rectification of tidal currents on the sides of Georges Bank. J. Phys. Oceanogr. 10: 1400–1416.

Loder, J. W., C. K. Ross, and P. C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. 45: 1860–1885.

Lonquet-Higgins, M. S. 1969. On the transport of mass by time-varying ocean currents. Deep Sea Res. 16: 431–447.

Lively, R. R. 1984. Current meter, meteorological and sea-level observations off Cape Sable, Nova Scotia, Can. Tech. Rep. Hydrogr. Ocean Sci. 40: 494 p.

Marak, R. R., and J. B. Colton, Jr. 1961. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank–Gulf of Maine area, 1953. Spec. Sci. Rep. U.S. Fish. Wildl. Serv.-Fish. 398: 61 p.

Marak, R. R., J. B. Colton, Jr., and D. B. Foster. 1962a. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank–Gulf of Maine area, 1955. Spec. Sci. Rep. U.S. Fish. Wildl. Serv.-Fish. 411: 66 p.

Marak, R. R., J. B. Colton, Jr., D. B. Foster, and D. Miller. 1962b. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank–Gulf of Maine area, 1956. Spec. Sci. Rep. U.S. Fish. Wildl. Serv.-Fish. 412: 95 p.

Marsden, R. F. 1986. The internal tide on Georges Bank. J. Mar. Res. 44: 35–50.

Nelson, W. R., M. C. Ingham, and W. E. Schaaf. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull. 75: 23–41.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P-V. Reun. Cons. Int. Explor. Mer 183: 27–40.

PAGE, F. H., AND K. T. FRANK. 1989. Spawning time and egg stage duration in Northwest Atlantic haddock stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

PRESS, W. H., B. P. FLANNERY, S. A. TEUKOLSKY, AND W. T. VETTERLING. 1986. Numerical recipes: the art of scientific computing. Cambridge University Press, London, England. 818 p.

REDFIELD, A. C. 1939. The history of a population of *Limacina retroversa* during its drift across the Gulf of Maine. Biol. Bull. Mar. Biol. Lab., Woods Hole 76: 26–47.

SCOTT, J. S. 1982. Distribution of juvenile haddock around Sable Island on the Scotian Shelf. J. Northw. Atl. Fish. Sci. 3: 87–90.

SINCLAIR, M., M. J. TREMBLAY, AND P. BERNAL. 1985. El Nino events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42: 602–608.

SMITH, P. C. 1983. The mean and seasonal circulation off southwest Nova Scotia. J. Phys. Oceanogr. 13: 1034–1054.

1989a. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

1989b. Seasonal and interannual variability off southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

SMITH, S. D., AND E. G. BANKE. 1975. Variation of sea surface drag coefficient with wind speed. Quart. J. Royal Meteor. Soc. 101: 665–673.

SPAULDING, M. L., S. B. SAILA, E. LORDA, H. WALKER, E. ANDERSON, AND J. C. SWANSON. 1983. Oil-spill fishery impact assessment model: application to selected Georges Bank fish species. East Coast Shelf Sci. 16: 511–541.

TEE, K. T., P. C. SMITH, AND D. LEFAIVRE. 1987. Modelling and observations of the residual current off southwest Nova Scotia. *In* J. C. Nihoul and B. M. Jamart [ed.] Three-dimensional models of marine and estuarine dynamics. Elsevier Oceanography Series 45: 455–470.

TRITES, R. W., D. J. LAWRENCE, AND J. H. VANDERMEULEN. 1986. Modelling oil movements from the Kurdistan spill in Cabot Strait, Nova Scotia. Atmos.-Ocean 24(3): 253–264.

WALFORD, L. A. 1938. Effect of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank. Bull. U.S. Bur. Fish. XLIX, 73 p.

WRIGHT, D. G., D. A. GREENBERG, J. W. LODER, AND P. C. SMITH. 1986. The steady-state barotropic response of the Gulf of Maine and adjacent regions to surface wind stress. J. Phys. Oceanogr. 16: 947–966.

ZIMMERMAN, J. T. F. 1979. On the Euler-Lagrangian transformation and the Stokes drift in the presence of oscillatory and residual currents. Deep-Sea Res. 26A: 505–520.

Appendix

The barotropic circulation on continental shelves or in shallow seas is well described by the shallow water equations. Furthermore, if the tidal circulation is dominant, as in the Gulf of Maine, the degree of nonlinearity of the system is measured by the ratio, κ, of the characteristic tidal current speed, U_T, to the barotropic wave speed, $\sqrt{gh}$, where g is the gravitational constant and h is the depth. Thus if the frictionless equations of motion are scaled according to:

$$\begin{aligned} &(u,v) = \kappa\sqrt{gh}\,(u', v'), \\ \text{(A.1)}\quad &\zeta = \kappa h \zeta', \\ &(x, y) = k^{-1}(x', y')\ ;\ \omega/k = \sqrt{gh}/\sqrt{1-\hat{f}^2}, \\ &t = \omega^{-1}t'\ ;\ \hat{f} = f/\omega, \end{aligned}$$

where $[u(x, y, t), v(x, y, t)]$ are the horizontal Eulerian velocity components, ζ is sea level and (ω, k) are the characteristic frequency and wave number, the dimensionless forms are (dropping primes):

$$\text{(A.2a)}\quad u_t + \gamma\kappa(uu_x + vu_y) - \hat{f}v = -\gamma\zeta_x$$

$$\text{(A.2b)}\quad v_t + \gamma\kappa(uv_x + vv_y) + \hat{f}u = -\gamma\zeta_y$$

$$\text{(A.2c)}\quad \zeta_t = \gamma\{[(1+\kappa\zeta)\,u]_x + [(1+\kappa\zeta)\,v]_y\}$$

where $\gamma = \sqrt{1-\hat{f}^2}$ and subscripts denote differentiation.

The Lagrangian velocity components, (u_L, v_L), are defined as the velocity of a labelled water parcel at time t, which was released from (x_o, y_o) at time t_o (Cheng et al. 1986). Thus

$$\text{(A.3a)}\quad u_L(x, y, t) = u(x_o + \kappa\xi, y_o + \kappa\eta, t)$$

$$\text{(A.3b)}\quad v_L(x, y, t) = v(x_o + \kappa\xi, y_o + \kappa\eta, t)$$

where the velocity and displacement (ξ,η) vectors have been scaled by $\kappa\sqrt{gh}$ and κ/k, respectively. The normalized displacements are defined by the integral equation:

$$\text{(A.4)}\quad (\xi, \eta) = \gamma \int_{t_0}^{t} [u(x+\kappa\xi\, y+\kappa\eta, t''), v(x+\kappa\xi, y+\kappa\eta; t'')]dt''$$

With appropriate initial and boundary conditions, equations (A.2) to (A.4) may be solved for ζ, u, v, u_L, v_L, ξ, and η. These equations differ from those of Cheng et al. (1986) by the factor γ in (A.2) and (A.4).

Sverdrup Wave

For $\kappa << 1$, the dependent variables may be expanded in powers of κ, e.g.

$$\text{(A.5)}\quad u = \sum_{j=0}^{\infty} u_j \kappa^j$$

At lowest order $(j=0)$, equation (A.2) yields an equation for sea level,

$$\text{(A.6)}\quad \zeta_{0_{tt}} + \hat{f}^2 \zeta_0 - \gamma^2(\zeta_{0_{xx}} + \zeta_{0_{yy}}) = 0$$

which has a free wave solution of the form,

$$\text{(A.7)}\quad \zeta_o = A \sin(t-x),$$

subject to the dispersion relation,

$$\text{(A.8)}\quad \hat{f}^2 + \gamma^2 - 1 = 0$$

It follows from equation (A.2) that $u_o = B\sin(t-x)$, $v_o = \hat{f}B\cos(t-x)$ and $A = \gamma B$. Thus choosing $B \equiv 1$ gives the elemental Sverdrup wave solution,

$$\begin{aligned} &\zeta_o = \gamma\sin(t-x) = \zeta_o' \cos t + \zeta_o'' \sin t \\ \text{(A.9)}\quad &u_o = \sin(t-x) = u_o' \cos t + u_o'' \sin t \\ &v_o = \hat{f}\cos(t-x) = v_o' \cos t + v_o'' \sin t \end{aligned}$$

where $u_o' = \zeta_o'/\gamma = -\sin x$, $u_o'' = \zeta_o''/\gamma = \cos x$, and $(v_o', v_o'') = \hat{f}(\cos x, \sin x)$. Again the factor γ is missing from the results of Cheng et al. (1986).

At higher order $(j = 1,2)$, Cheng et al. (1986) have shown that, in general, the Lagrangian residual current (u_{LR}, v_{LR}) is equal to the well-known Eulerian residual (u_{ER}, v_{ER}) and Stokes drift (u_{SD}, v_{SD}) components, plus a higher-order Lagrangian drift velocity, $\kappa\,(u_{LD}, v_{LD})$, i.e.

$$\text{(A.10a)}\quad u_{L_1} + \kappa\, u_{L_2} \equiv u_{LR} = u_{ER} + u_{SD} + \kappa\, u_{LD} + 0(\kappa^2),$$

$$\text{(A.10b)}\quad v_{L_1} + \kappa\, v_{L_2} \equiv v_{LR} = v_{ER} + v_{SD} + \kappa\, v_{LD} + 0(\kappa^2),$$

where,

$$\text{(A.11a)}\quad u_{SD} = \langle (u_{0_x})_0\, \xi_0 \rangle + \langle (u_{0_y})_0\, \eta_0 \rangle,\ \xi_0 = \gamma \int_{t_0}^{t} u_0(x_0, y_0, t'')\, dt''$$

(A.11b) $v_{SD} = \langle (v_{0_x})_0 \, \xi_0 \rangle + \langle (v_{0_y})_0 \, \eta_0 \rangle, \; \eta_0 = \gamma \int_{t_0}^{t} v_0(x_0, y_0, t'') \, dt''$

with $<(\;)>$ representing the time average over a tidal period, $(\;)_o$ indicating evaluation at (x_o, y_o), and where,

(A.12a) $u_{LD} = u_{LD}' \cos \theta_0 + u_{LD}'' \sin \theta_0,$

(A.12b) $v_{LD} = v_{LD}' \cos \theta_0 + v_{LD}'' \sin \theta_0$

with θ_0 as the initial phase angle of the wave. The formulae (A.11) for the Stokes drift velocity are the same as those given by Cheng et al. (1986), except for the factor γ multiplying the integrals. Similarly, the coefficients in (A.12) are the same as in Cheng et al. (1986; their equation (22)), except for multiplication by γ. Note that the lowest-order residual currents, (u_{ER}, v_{ER}) and (u_{SD}, v_{SD}), are independent of the θ_0, whereas the Lagrangian drift correction, $\kappa \, (u_{LD}, v_{LD})$, traces out an ellipse on a hodograph plane (Cheng et al. (1986); their figure 5).

To test the particle trajectory model, the Eulerian velocity field was taken to be the Sverdrup wave solution (A.9), with $\hat{f} = 0.4$ and $\kappa = 0.2, 0.4$. After one or two tidal periods ($T = 12.5$ h), the end points of the model trajectories for particles released at various initial phases of the tide traced, to within 3%, the appropriate displaced ellipse defined by substituting (A.9) into (A.10) to (A.12), i.e.,

(A.13a) $u_{LR} = 0 + \gamma/2 + \gamma\kappa \sin(\theta_0 - x_o - \pi)/2,$

(A.13b) $v_{LR} = 0 + 0 + \gamma \, \kappa \, \hat{f} \cos(\theta_0 - x_o - \pi)/2.$

Note that these displacements differ from those derived by Cheng et al. (1986) by the factor γ, which for this case had a numerical value of 0.92.

Structure and Interannual Variability of the Plankton and its Environment off Southwest Nova Scotia in Late Spring and Early Summer[1]

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Consistent alongshore and/or onshore–offshore gradients in temperature, salinity, and inorganic nutrient were observed off southwest Nova Scotia in June/July, 1981–85. The distributions were established primarily by mixing of relatively warm, high-salinity, nutrient-rich Slope Water with the cold, low-salinity, nutrient-poor water of the Nova Scotia Current. Tidal mixing and frontal dynamics were of secondary importance. Consistent with the distribution of nutrient and the earlier onset of stratification offshore, chlorophyll a concentrations were generally highest offshore and lowest inshore, and the distributions of zooplankton displacement volume and of dominant copepod species were similar. Salinity, nutrient, and chlorophyll a concentrations and the abundance of zooplankton were all generally higher throughout the spring of 1985 than in 1983–84. In 1985, there was greater upwelling and Slope Water influence and decreased flow of the shelf current. This was associated with a reversal of the North Atlantic atmospheric pressure anomaly field, which led to predominantly offshore and southwest alongshore winds in winter and spring, 1985. Correlations of recruitment to northwest Atlantic cod (*Gadus morhua*) stocks with wind and North Atlantic atmospheric pressure anomalies (Koslow et al. 1987) may be based upon the wind's influence on nutrient availability and plankton abundance.

Au cours des mois de juin et de juillet de 1981 à 1985, on a observé des gradients uniformes de la température, de la salinité et des teneurs en éléments nutritifs inorganiques du large vers la côte et vice versa ainsi que le long de la côte sud-ouest de la Nouvelle-Écosse. Le mélange des eaux relativement chaudes de la pente continentale, à salinité élevée et riches en éléments nutritifs, avec les eaux froides du courant de la Nouvelle-Écosse, à faible salinité et pauvres en éléments nutritifs, est en grande partie à l'origine des gradients. Le brassage des marées et la dynamique des fronts jouent un rôle secondaire. En accord avec la distribution des éléments nutritifs et l'apparition précoce d'une stratification des eaux hauturières, les concentrations de chlorophylle a étaient généralement plus élevées dans les eaux hauturières et plus faibles dans les eaux côtières tandis que les distributions du volume de déplacement du zooplancton et des principales espèces de copépodes étaient semblables. La salinité, les teneurs en éléments nutritifs, les concentrations de chlorophylle et l'abondance du zooplancton étaient généralement plus élevées au cours du printemps 1985 qu'en 1983–84. En 1985, les remontées d'eau profonde et les eaux de la pente ont eu une plus forte influence tandis que l'intensité du courant de la plateforme a diminué. Ces phénomènes étaient associés à un renversement de l'anomalie de la pression atmosphérique dans l'Atlantique nord qui a entraîné des vents soufflant surtout de terre et le long de la côte sud-ouest au cours de l'hiver et du printemps 1985. Les corrélations entre le recrutement de la morue franche (*Gadus morhua*) aux stocks de l'Atlantique nord-ouest et le vent ainsi que les anomalies de la pression atmosphérique dans l'Atlantique nord (Koslow et al. 1987) sont peut-être basées sur l'influence qu'à le vent sur la disponibilité d'éléments nutritifs et l'abondance du phytoplancton.

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The oceanography off southwestern Nova Scotia is regulated by several factors: tidal mixing, upwelling, winter cooling and summer warming, the southwesterly flow along the shelf of the Nova Scotian Current, and Slope Water intrusions (Fig. 1).

Strong tidal currents establish a predictable onshore–offshore structure. The inshore region is well mixed throughout the year, leading to development of a front in summer at approximately 100 m depth between the inshore and stratified offshore waters (Garrett et al. 1978). Higher concentrations of chlorophyll *a* are found seaward off the front in summer, due to nutrient input into a region of water column stability (Fournier et al. 1984). However, high interannual variability in summer chlorophyll *a* concentrations off southwest Nova Scotia (Fournier et al. 1984) and the frequent occurrence of patches outside the frontal area containing higher salinity and high concentrations of nutrients and chlorophyll *a* have been related to Slope Water (SW) intrusions rather than tidal mixing (Denman and Herman 1978; Fournier et al. 1984).

Mass balance models indicate that the flux of nutrients onto the Scotian Shelf and into the Gulf of Maine is primarily regulated by the admixture of relatively warm, deep, high-salinity, nutrient-rich SW (temperature (T) = 5–14°C depending upon whether it is of Labrador or Gulf Stream origin; salinity (S) >34.5 (Hopkins and Garfield 1979)) with the relatively cool, fresh, nutrient-poor, near-surface water of the Nova Scotia Current (SSW) (T = 0–10°C; S = 31–33 (Hopkins and Garfield 1979)) (Fournier et al. 1977; Houghton et al. 1978; Smith 1978; Pastuszak et al. 1982; Schlitz and Cohen 1984; Ramp et al. 1985). Off southwest Nova Scotia and in the Gulf of Maine generally, variable pulses of Slope Water enter through the Northeast Channel between Browns and Georges Banks (Bigelow 1927; Brooks 1985; Ramp et al. 1985). In winter and early spring, these pulses are associated with offshore and southwesterly alongshore winds (Ramp et al. 1985). Offshore warm core rings may also be associated with SW intrusions (Brooks 1987; but see also Ramp et al. 1985; Smith 1989). The flow of the coastal Nova Scotia Current into the Gulf of Maine is also seasonal and highly variable, peaking in winter or spring and virtually ceasing in summer (Bigelow 1927; Smith 1983, 1989). Vernal circulation in the Gulf of Maine is largely driven by relative inputs of SW and SSW (Brooks 1985). However, the more general role played by varying fluxes of shelf and slope water masses in regulating interannual variability in biological productivity off southwest Nova Scotia is not clear.

Upwelling also influences nutrient distributions off southwest Nova Scotia. Upwelling has been inferred in the area from seabed drifter and current meter observations and is correlated with southwest alongshore winds (Lauzier 1967; Smith 1983, 1989).

Bearing in mind the dominant processes regulating the oceanography of the region, we examine here, first, the onshore–offshore and alongshore distribution of physical, chemical, and planktonic variables off southwest Nova Scotia in the late spring and early summer (June and July), 1981–85. We next examine interannual variability in these variables in relation to varying atmospheric and oceanographic conditions.

Methods

Cruises were conducted off southwest Nova Scotia July 10–14, 1981, in June 1982, and once each month from February

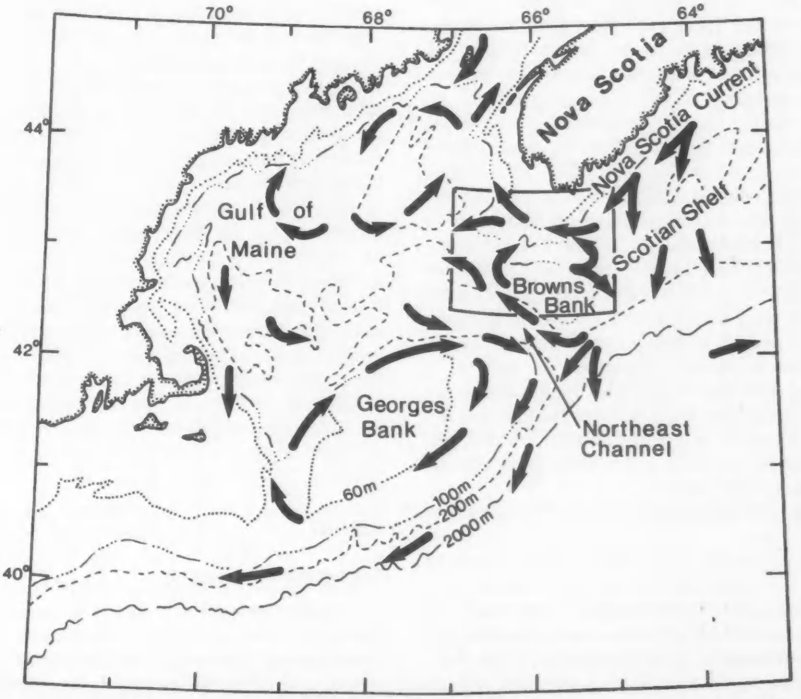

FIG. 1. Northwest Atlantic showing major topographic features and circulation patterns. Adapted from a figure by R. Trites, Bedford Institute of Oceanography, Dartmouth, N.S.

through June 1983–85. The location of transects differed somewhat between 1981–82 and 1983–85 cruises (Fig. 4, below), but in all cruises, two onshore–offshore transects crossed Browns Bank and two to three others were situated west of the bank. On each transect, stations were occupied in the following oceanographic regimes: the shallow, tidally well-mixed inshore region; the deeper, potentially stratified water (depth >100 m); the tidally-induced frontal region that is established in late spring; over Browns Bank; and along the bank edge. The well-mixed, frontal, and stratified regions were initially defined in terms of the stratification parameter

$$(1)\quad S = \mathrm{Log}_{10}[B \cdot H \cdot U^{-3}],$$

where B is the buoyancy flux, H is water depth, and U is tidal velocity (Garrett et al. 1978). The water was considered well-mixed in areas where $S<1.0$; stratified where $S>2.0$; and the frontal region where $1.0 \leq S \leq 2.0$, based upon Garrett et al. (1978) and a plot (not shown here) of S against the difference in density between the surface and 50 m.

At each station, a vertical profile of temperature and salinity was obtained with a Guildline conductivity–temperature–depth (CTD) sensor, and water samples were obtained with a rosette sampler at discrete depths (typically at 10-m intervals from 0–50 m and 25-m intervals thereafter) from the surface to 150 m or within 20 m of the bottom. Chlorophyll *a*, salinity, and nitrate were analyzed from the water samples (Strickland and Parsons 1968). An oblique zooplankton tow from 150 m (or within 20 m of the bottom) to the surface was taken on each station with a Bongo frame fitted with 60-cm diameter, 0.333-mm mesh nets and centrally-mounted General Oceanics flowmeters. Tows were timed and velocities (typically 2 knots ($1\ \mathrm{m \cdot s^{-1}}$)) recorded to provide a check on flowmeter readings.

In analyzing zooplankton samples from June/July cruises, medusae and ctenophores (primarily *Pleurobrachia pileus*) were removed and enumerated due to their relatively large volume/dry weight and volume/carbon ratios, and the displacement volume of remaining zooplankton determined. All copepods were enumerated to genus or species in sample aliquots obtained with Stempel pipette or Folsom splitter. Sufficient aliquots were analyzed until at least 30–50 of the more numerous taxa had been counted (Cassie 1968). The abundance of zooplankton is expressed as the number per square metre based on the volume filtered and depth of tow. For February–May cruises, ctenophores were enumerated to $\log_{10}$ categories (i.e. 1–9, 10–99, 100–999, >1000) but were not removed from samples prior to measuring displacement volume, so displacement volumes from samples containing more than 100 ctenophores were not used in subsequent analyses.

Two-way analyses of variance (ANOVA) (by year and oceanographic regime and by year and transect) were used to test for:

1) significant differences in the distribution of physical, chemical, and biological variables either alongshore (i.e. by transect) or by oceanographic regime;

2) interannual differences in the levels of these variables over the study area; and

3) consistency from year to year in the distribution pattern of these variables.

Prior to performing ANOVA, the variables were examined for normality using the Kolmogorov-Smirnov one-sample test for goodness of fit, and for homogeneity of variance with Bartlett's and Cochran's tests (Norusis 1988). As a result, all variables except salinity and σ_t were $\log_{10}$ transformed. Nonparametric Kruskal-Wallis one-way ANOVA was used when variables showed significant heteroscedasticity after the $\log_{10}$ and other transformations. Stations containing zeros for planktonic variables were omitted from analyses of those variables; and data for *P. pileus* were not analyzed with ANOVA due to the high incidence of zeros.

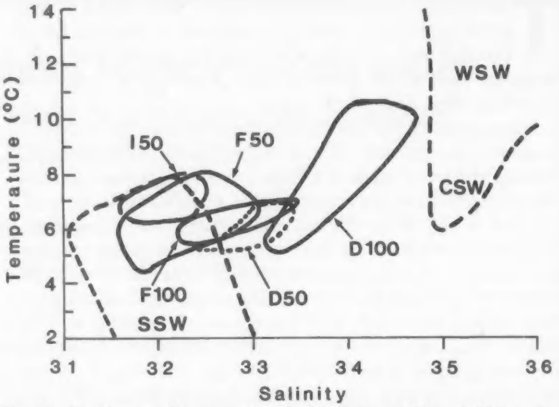

FIG. 2. Envelopes of temperature and salinity at 50 and 100 m for stations in the inshore (I), tidal front (F), and offshore (D) (i.e. seaward of Browns Bank) regions from June–July cruises, 1981–85. Envelopes for warm and cold Slope Water (WSW, CSW) and Scotia Shelf Water (SSW) (dashed lines) from Hopkins and Garfield (1979).

In carrying out two-way ANOVA, we first examined whether the variable's spatial distribution (either alongshore by transect or onshore–offshore by oceanographic regime) was consistent between years (i.e. the 'interaction effect' between year and transect or oceanographic regime). If the distribution was consistent (i.e. interaction nonsignificant ($p>0.05$)), we tested for significant spatial pattern over all years (i.e. significant differences in the means among transects or oceanographic regimes, taking into account interannual differences) and for interannual differences over all regions (i.e. significant differences in the means among years, taking into account the spatial distribution). If the main effects were significant, the significance of differences between particular years, transects, or oceanic regions was examined with the least significant difference (LSD) test, and the significance level was set at $p<0.005$ based on the Bonferoni correction for multiple comparisons. If the spatial distribution was not consistent between years, the distribution was examined separately for each year, and interannual differences were examined separately for each oceanographic regime. Only data from 1983–85 were used to test for differences among transects due to different transect placement in 1981–82 (see Fig. 4). The regression model of ANOVA was used, which is suitable for unbalanced experimental design (i.e. different numbers of cases per treatment cell) (Milliken and Johnson 1984; Norusis 1988).

Results

Temperature and Salinity

In late spring–early summer, consistent patterns of temperature and salinity were maintained off southwest Nova Scotia primarily through the competing influence of water masses of Scotian Shelf and slope origin, as well as the effects of tidal mixing and solar warming. A plot of temperature and salinity for June–July, 1981–85 from the nearshore, frontal, and

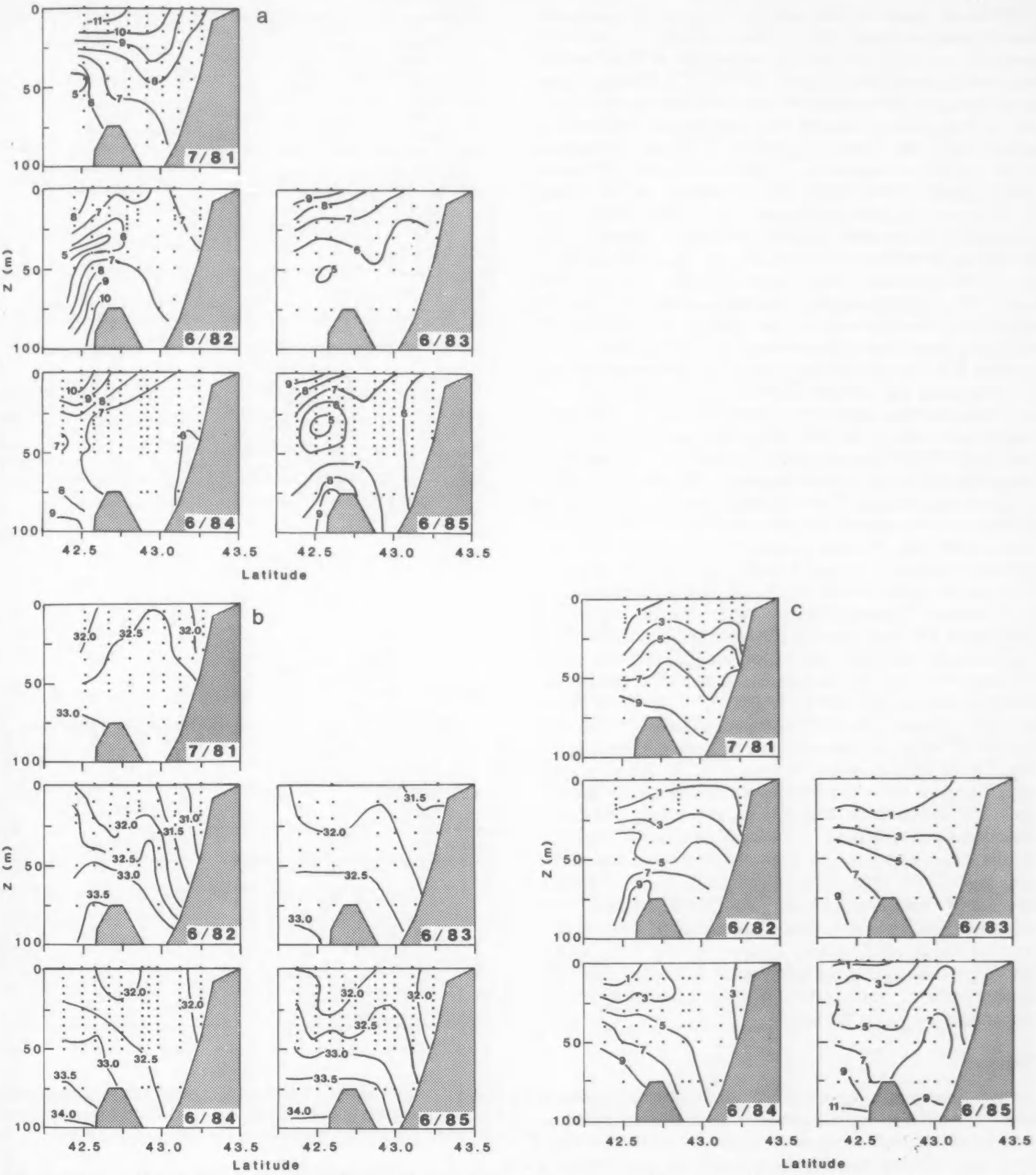

FIG. 3. Vertical profiles along approximately 66°W from the nearshore (far right) across Browns Bank to the offshore of (a) temperature (°C), (b) salinity, and, (c) nitrate concentration (μM).

offshore zones at 50 and 100 m indicated a gradient in the influence of these water types (Fig. 2). Thus the nearshore region, which is dominated by SSW, was cool and fresh, and the deep water in the Northeast Channel, where SW enters the Gulf of Maine (Bigelow 1927; Brooks 1985; Rampe et al. 1985), relatively warm and saline. These water types can also be seen in a vertical section extending offshore at approximately 66°W, in which cool water with salinity ≤32, characteristic of SSW, and nitrate concentrations ≤3 μM was concentrated nearshore and in the surface layer; relatively warm water with salinity >33 and nitrate concentrations >7 μM extended onto the shelf from the slope (Fig. 3). As a result, there was a significant onshore–offshore gradient in salinity at 50 m, though not at 10 m, where the relatively deep SW has little influence

(Fig. 4b, 5b; Table 1). Cool fresh SSW entered the study area from the northeast, leading to significant alongshore (east–west) gradients in salinity at 10 m and of temperature at 50 m (beneath the solar-warmed layer) (Fig. 4a, 5b; Table 2). Solar warming of the surface water was only evident offshore of Browns Bank, due to tidal mixing inshore. The temperature minimum at approximately 50 m was characteristic of Maine Intermediate Water (MIW), a remnant of winter-cooled Gulf of Maine Surface Water (MSW) (Hopkins and Garfield 1979; Brooks 1985), which was present offshore (Fig. 3a). As a result, there was a significant onshore–offshore gradient in temperature near the surface (10 m) but not at 50 m (Fig. 4a, 5a; Table 1). These underlying temperature and salinity patterns were observed consistently, highlighting the importance of these processes in establishing the structure of the marine environment off southwest Nova Scotia (interactions not significant ($p>0.05$) between year and distribution by transect and oceanic regime for temperature and salinity at 10 and 50 m (Tables 1,2)).

Although overall patterns of temperature and salinity were similar each year in the late spring/early summer, 1981–85, there was significant interannual variability in regional temperature and salinity due to varying contributions of the shelf and slope water masses (Table 1). Selecting the 34 isohaline as indicative of SW influence (Hopkins and Garfield 1979; Brooks 1987), water with this characteristic was only found in 1984 and 1985 at depths ≤100 m (Fig. 2b). In June 1984, this was related to the presence of a warm core ring at the entrance of the Northeast Channel (Brooks 1985), but no significant intrusion of SW was observed. However, in June 1985, there was generally increased salinity off southwest Nova Scotia (Table 1). At 50 m, the 33 isohaline, which characterizes the boundary between near-surface waters (SSW, MSW, or MIW) and water influenced by SW (Hopkins and Garfield 1979), was only found within the channel north of Browns Bank in 1985 (Fig. 5b). As seen in a vertical section (Fig. 3b), higher salinity water extended from the Northeast Channel across Browns Bank and the northern channel. In 1981, there were also somewhat elevated salinities at 10 and 50 m (Fig. 4b, 5b; Table 1), but these appear to indicate the relatively diminished influence of SSW rather than an enhanced flux of SW, since there was no evidence of higher salinity at depth either from our cruise (Fig. 3b) or in the data of Mountain and Jessen (1987) from the Northeast Channel. Temperatures in 1981 appear elevated but this reflects the later date of the cruise: seasonally adjusted data of Smith (1989) do not indicate significant temperature anomalies that spring.

Nutrients

The influence of high-salinity SW on the nutrient content of water off southwest Nova Scotia can be seen from the correlation of salinity and nitrate concentration for subsurface water ($r=0.69$, $p<0.001$; Fig. 6). As a result, the distribution of nitrate at 50 m reflected the confluence of shelf and slope water influences off southwest Nova Scotia. A significant onshore–offshore gradient in nitrate concentration at 50 m was found consistently, lowest values occurring inshore, where the influence of fresh, nutrient-poor SSW was greatest, and highest values being offshore, where SW influence was strongest (Fig. 5c, Table 1). An alongshore gradient in nutrient concentration was observed only in 1985 due to the intrusion of saline, high-nutrient water into the study area through the deeper channels (Fig. 5c; Table 2). Vertical sections of nitrate and salinity also indicate possibly enhanced upwelling of saline, nutrient-rich water shoreward of Browns Bank in 1985 (Fig. 2b,c: isopycnals, not shown here, parallelled the isohalines).

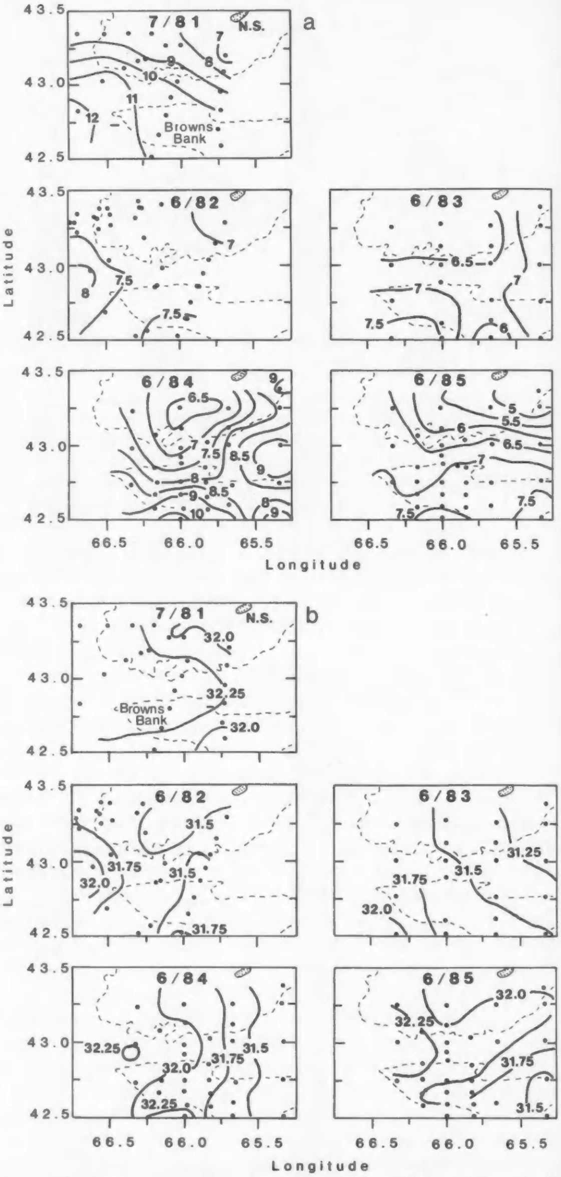

FIG. 4. Contours of (a) temperature (°C) and (b) salinity at 10-m depth (near surface layer) from June/July cruises, 1981–85 (month and year as shown). The dashed lines indicate the 100-m depth contour.

Interannual variability in mean nitrate concentration off southwest Nova Scotia was consistent with observed differences in shelf and slope water mass contributions and possible upwelling. As observed for salinity, nitrate concentrations at 50 m were higher in June 1985 and July 1981 than in June 1982–84 (Fig. 5c; Table 1). Nitrate concentrations at 10 m in 1981 and 1985 were also higher (Table 1). Due to a combination of weak vernal thermal stratification, tidal mixing, upwelling, and

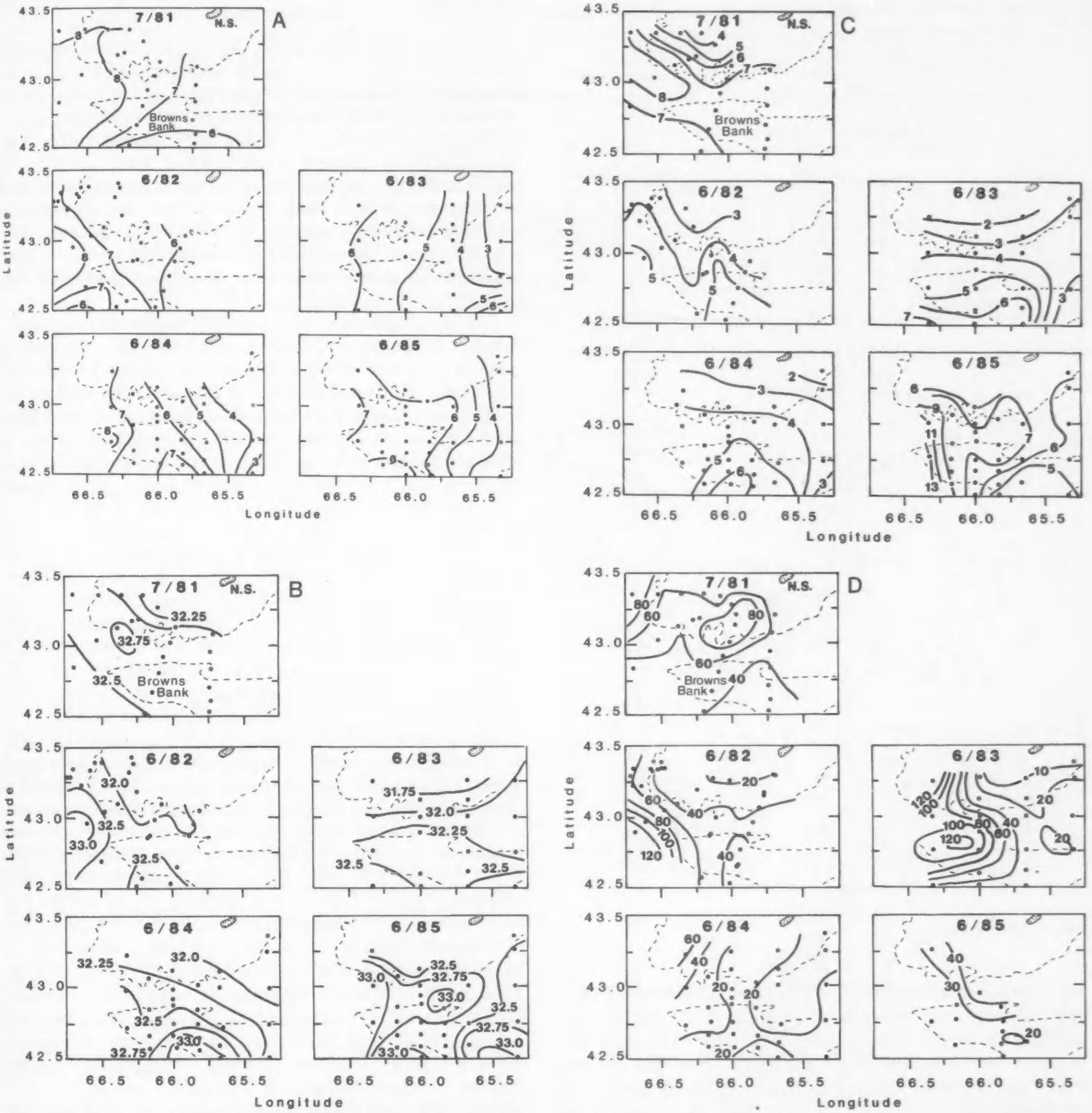

FIG. 5. Contours of (a) temperature (°C), (b) salinity, and (c) nitrate concentration (μM) at 50-m depth; (d) chlorophyll *a* concentration (mg/m^2) integrated over the water column; and (3) zooplankton displacement volume (mL/m^2) by month and year as shown. The mean abundance (number/m^2) for all June–July cruises, 1981–85 of (f) *Calanus finmarchicus*; (g) *Metridia lucens*; and (h) *Pseudocalanus* spp. The dashed lines indicate the 100-m depth contour.

other water mass exchange processes, nutrient concentrations in the near-surface layer still reflected nutrient levels in deeper water, although heightened spring phytoplankton production had been noted since March–April (Fig. 7; Perry et al. 1989). Seasonal and interannual variation in phosphate concentration generally followed that of nitrate (Fig. 7).

Chlorophyll *a*

The distribution of chlorophyll *a* in late spring/early summer tended to follow gradients in the distribution of water masses and nutrients. Mean chlorophyll *a* concentrations in the water column generally increased alongshore, reflecting the alongshore gradient in SW contribution to water on the shelf (Fig. 5d; Table 2). A consistent onshore–offshore pattern in the distribution of chlorophyll *a* did not emerge, as indicated by the significant interaction between oceanographic regime and year (Table 1). However, in June 1982 and 1985, when there was an onshore–offshore gradient, highest mean concentrations of chlorophyll *a* were observed in deeper areas, which contained

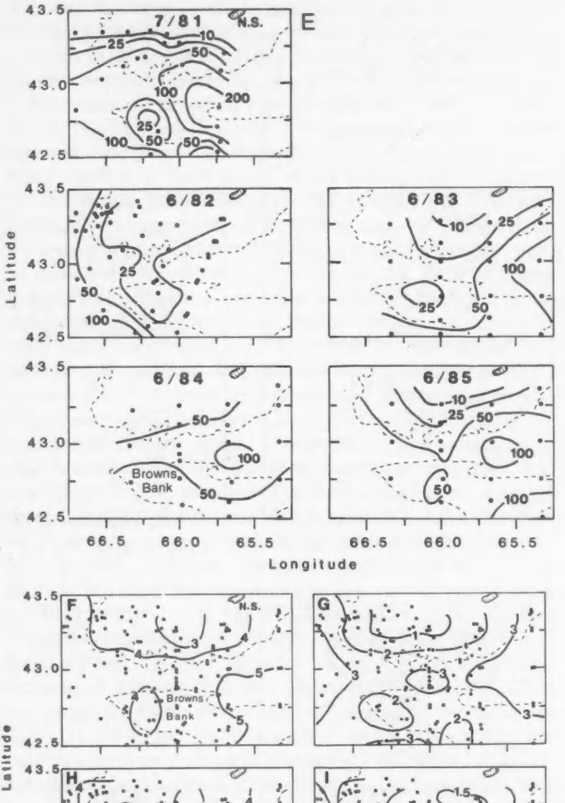

FIG. 5. *(continued)*

the highest subsurface (50 m) nutrient concentrations and were most strongly stratified (Fig. 3, 5c,d; Table 1). Intermediate levels of chlorophyll *a* were found at the edge of the bank and at the tidal front, and lowest concentrations were found inshore, which was both least stratified and contained the lowest nutrient concentrations.

There were significant interannual differences in mean June/July chlorophyll *a* concentration off southwest Nova Scotia, although these differences were not entirely consistent across all regions (Fig. 5d; Table 1). The highest mean levels of chlorophyll *a* occurred in most areas in 1981, which is consistent with the hypothesis that somewhat higher nutrient concentrations at that time resulted from decreased inflow of low-nutrient SSW. Low chlorophyll *a* concentrations in June 1985 may have resulted from insufficient time for phytoplankton growth to have incorporated the ongoing nutrient pulse. However, the mean concentration of chlorophyll *a* in 1985 had declined since April, when the highest mean concentration over the entire study period was observed (Fig. 7; Perry et al. 1989). This suggests that another factor was responsible, which we examine next.

Zooplankton

Zooplankton data were highly variable, but overall zooplankton displacement volume and the abundance of *Calanus finmarchicus*, the most abundant species, and *Metridia lucens* were generally found in highest concentrations over deep water, on the edge of Browns Bank, and in the frontal region (Fig. 5f–h; Table 1). Lowest concentrations were consistently observed inshore, and relatively low concentrations also tended to occur over Browns Bank. *Pseudocalanus* did not exhibit a clear distributional pattern (Fig. 5h; Table 1). Neither zooplankton displacement volume nor the abundance of any of the three major species showed a significant alongshore gradient in late spring (Fig. 5e–h; Table 2).

Overall zooplankton displacement volume and the abundance of *C. finmarchicus* in June were highest in most areas in 1985, followed by 1984, and lowest in 1981 and 1982 (Fig. 5e,f; Table 1). The abundance of *Pseudocalanus* followed a similar rank order of abundance. Concentrations of chlorophyll *a* were highest in late spring of 1981 and 1982 and lowest in 1984 and 1985, which suggests an inverse relationship between phytoplankton and zooplankton abundance due to the impact of zooplankton grazing. This can be seen in a plot of annual means by oceanographic regime of the abundance of *C. finmarchicus* against concentration of chlorophyll *a* (Fig. 8). The scatterplot appears wedge-shaped due to low levels of both phytoplankton and zooplankton in the tidally-mixed inshore region, where lack of stratification limits phytoplankton production and hence zooplankton population growth. If the inshore area is deleted, there is a significant negative correlation between the chlorophyll *a* concentration and abundance of *C. finmarchicus* (Kendall's Tau $= -0.27$, $n = 19$, $p < 0.05$).

The distribution of the major planktonic predator in the area in spring, the ctenophore *Pleurobrachia pileus*, was inversely related to that of the crustacean zooplankton (Fig. 9: Kendall's Tau $= -0.26$, $n = 25$, $p < 0.05$), being most abundant inshore and least abundant offshore (Fig. 5i). Consistent with previous studies of ctenophore ecology in the area (Anderson 1974; Milne 1984), Frank (1986) showed that predation by *P. pileus* contributed significantly to the mortality of crustacean zooplankton on Browns Bank in 1983, when the ctenophore was anomalously abundant there, but not in 1984, when it was at levels more typical of noninshore areas (i.e. $<5/m^2$) (Fig. 9). Thus inshore, where ctenophore abundance was typically greater than $10/m^2$, ctenophores likely contributed, along with low levels of phytoplankton, to the low abundance of zooplankton in that region. However, *P. pileus* was generally not sufficiently abundant beyond the well-mixed inshore region to significantly affect zooplankton abundance. We note that if the inshore data were removed, the relationship between ctenophore abundance and zooplankton displacement volume was no longer significant (Kendall's Tau $= -0.07$, $n = 20$, $p = 0.32$).

Productivity appeared higher in the spring of 1985 based upon data from monthly cruises, February–May, 1983–85 (Fig. 7; Perry et al. 1989). Mean concentrations of nutrients and chlorophyll *a* off southwest Nova Scotia were greater in 1985 than 1983 or 1984 from March through May. Zooplankton displacement volumes were higher in May and June of 1985 than in 1983 and 1984, which suggests that the decline in June 1985 of mean levels of chlorophyll *a* was related to zooplankton grazing. The cruise in March 1985 (not shown here) indicated that another pulse of saline, nutrient-rich water from the Northeast Channel entered the study area through the channel north of

TABLE 1. Results of analysis of variance (ANOVA) to test for differences among years (YR) (1981–85) and oceanographic regions (REG) of variables contoured in Figs. 4 and 5. Bar over years or regions indicates they are not significantly different (LSD test, $p > 0.005$). See Methods for details of analysis. H = results of test for heteroscedasticity; I = inshore; F = tidal front; O = offshore; BT = Browns Bank; BE = bank edge. DV = zooplankton displacement volume; n = number of data points; ns = not significant; ? = $p < 0.10$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Variable	(n)	H	Interaction (YR × REG)	Region effect	Year effect
S (10 m)	(169)	ns	ns	ns	82 83 84 85 81 ***
T (10 m)	(172)	***	ns	I F BT O BE ***	85 83 82 84 81 ***
S (50 m)	(158)	**	ns	I F O BT BE ***	82 83 84 81 85 ***
T (50 m)	(159)	*	ns	ns	83 85 84 82 81 ***
NO_3 (50 m)	(155)	*	ns	I F BE BT O **	83 82 84 81 85 ***
Chl (mg/m^2)	(157)	***	***	1981, 1983–84: ns 1982: I BT F BE O*** 1985: I BT F Be O ?	I: 83 82 85 84 81 ? F: 85 84 83 82 81 ? BT: 85 84 82 83 81** BE: 84 85 82 83 81*** O: 84 83 85 81 82 ***
DV	(161)	***	**	1984–85: ns 1981: I BT BE O F* 1982: I BTY F BE O*** 1983: I F BT BE O **	I, O: ns F: 83 82 85 84 81 ** BT: 82 81 83 84 85** BE: 81 82 84 85 83?
Calanus	(159)	*	**	1981: I BT BE F O ** 1982: I BT F BE O*** 1983: I F BT O BE ? 1984: I BE O BT F ? 1985: ns	I: 81 83 82 84 85** F: 83 82 81 85 84 * BT: 81 82 83 84 85** BE: 82 81 84 83 85** O: ns
Pseudocalanus	(156)	***	ns	ns	81 82 83 85 84 ***
Metridia	(126)	**	ns	I BT F BE O ***	82 81 83 85 84 ***

TABLE 2. Results of analysis of variance (ANOVA) to test for alongshore differences in distribution of variables contoured in Figs. 4 and 5, 1983–85, based on two-way ANOVA by transect (T) (numbered consecutively from east to west) and year (YR). Significance of transect effect is based on nonparametric Kruskal-Wallis (K-W) test for variables exhibiting significant heteroscedasticity (H) (Bartlett's test). Bar over transects indicates they are not significantly different. See Methods for further details of analytical method. DV = zooplankton displacement volume; n = number of data points; ns = not significant; ? = $p < 0.10$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Variable	(n)	H	Interaction (YR × T)	Transect effect
S (10 m)	(62)	ns	ns	$1 < 2 < 3$ **
T (10 m)	(63)	ns	ns	ns
S (50 m)	(56)	ns	ns	ns
T (50 m)	(56)	***	ns	$1 < 2 < 3$ **
NO_3 (50 m)	(58)	ns	*	1983: ns 1984: ns 1985: $2 < 1 < 3$?
Chl (mg/m^2)	(47)	*	ns	$1 < 2 < 3$ **
DV	(60)	ns	ns	ns
Calanus	(60)	ns	ns	ns
Pseudocalanus	(59)	ns	ns	ns
Metridia	(44)	ns	ns	ns

Browns Bank. The cruises in March and June 1985 were the only ones in which SW was observed actively entering the shelf area.

Discussion

Plankton Distribution

Not unexpectedly, the spatial distribution of nonconservative variables (i.e. phytoplankton and zooplankton, and to some extent of nutrient) was not as consistent between years as that of conservative physical oceanographic properties. However, in the late spring period, the primary influence of physical oceanography on the distribution of nutrient and biological

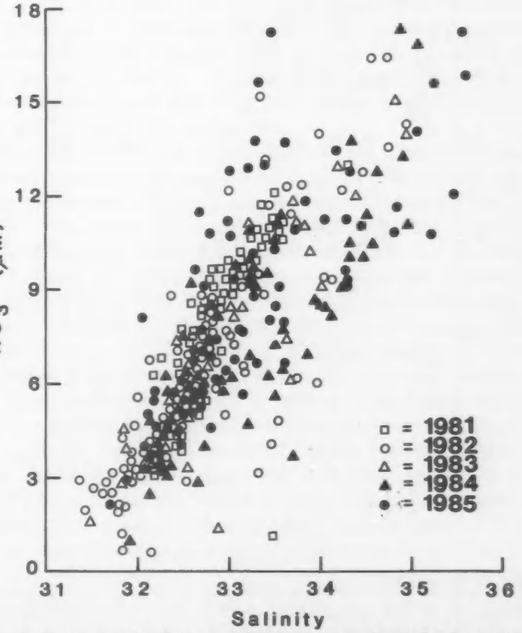

FIG. 6. Scatterplot of salinity and nitrate concentration at depths greater than 50 m from cruises in June–July, 1981–85 by year.

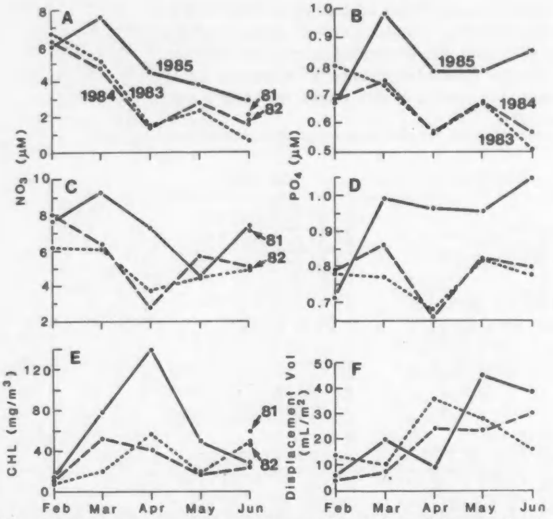

FIG. 7. Means over the study area for monthly cruises (February–June), 1983–85 of (a) nitrate and (b) phosphate concentration (µM) at 10 m; (c) nitrate and (d) phosphate concentrations at 50 m; (e) chlorophyll *a* concentration (mg/m²) integrated over the water column; and (f) median zooplankton displacement volume (mL/m²).

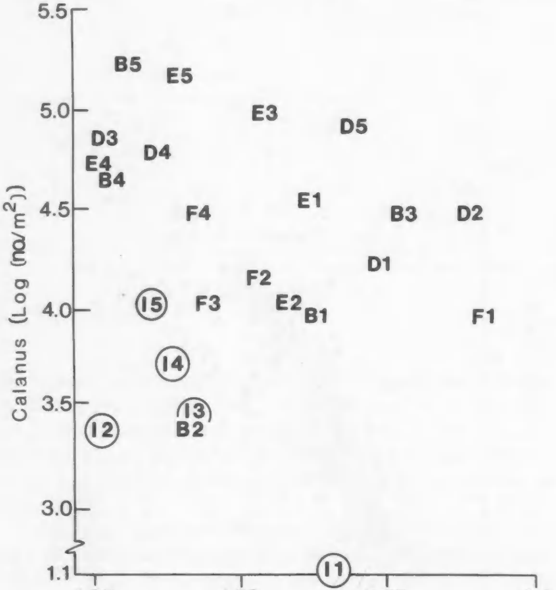

FIG. 8. Scatterplot of the mean abundance per square metre of *Calanus finmarchicus* and concentration of chlorophyll *a* by oceanographic region (I = inshore; F = tidal front; B = Browns Bank; E = edge of Browns Bank; D = deep) and year (1–5 = 1981–85). Note the log–log scale. Values from inshore region are circled.

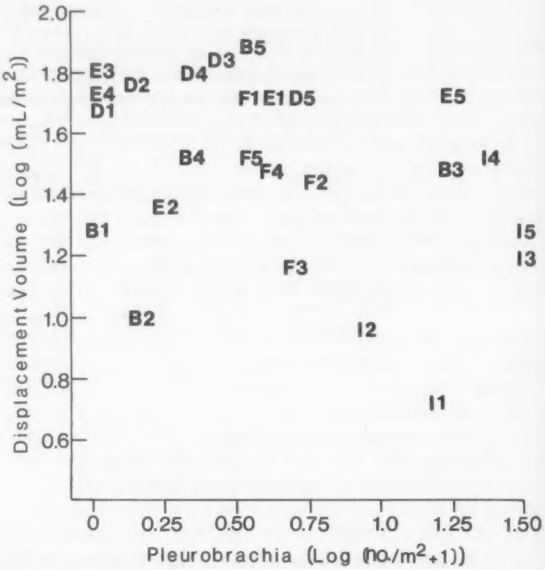

FIG. 9. Scatterplot of the mean zooplankton displacement volume and abundance of the ctenophore *Pleurobrachia pileus* by oceanographic region (I = inshore; F = tidal front; B = Browns Bank; E = edge of Browns Bank; D = deep) and year (1–5 = 1981–85).

variables could be clearly discerned. This can be seen by focussing initially on the distribution of zooplankton.

Zooplankton displacement volume and the abundance of dominant species (i.e. *C. finmarchicus* and *M. lucens*) were greatest from mid-shelf (i.e. offshore of the tidal front at ~100 m) to the slope in late spring, as previously described for the Gulf of Maine (Bigelow 1926), the Scotian Shelf (Tremblay and Roff 1983), and the northeastern United States (Judkins et al. 1979). This pattern appeared related primarily to the distribution of phytoplankton, which at this time of year was still found in highest concentrations offshore, where nutrient concentrations were greatest and stratification first occurred, thereby permitting development of the spring bloom (Perry et al. 1989). Thus the dominance in spring of these copepods, which overwinter in deeper water, may be related to the initial development there of their food resource.

The distribution of larger copepods also appeared inversely related to that of the ctenophore, *P. pileus*, which Bigelow (1926) first described as occurring in dense concentrations in spring in the inshore region off southwest Nova Scotia. The inverse distributional pattern of ctenophores and the larger zooplankton is consistent with Greve's (1977) hypothesis that *Calanus* and *Pleurobrachia* exclude each other through predation on each other's early life history stages. Ctenophore densities in late spring in the well-mixed inshore region, but not offshore, were generally at levels that would lead to significant copepod mortality (Anderson 1974; Milne 1984; Frank 1986).

Interannual Variability

Due to the dynamic character of the oceanography off southwest Nova Scotia and the lack of long-term consistent sampling, most oceanographic studies have focussed on describing mean seasonal conditions rather than interannual variability in the region. Fournier et al. (1984) emphasized the importance of tidal mixing in regulating the mean pattern of summer stratification, nutrient availability, and phytoplankton abundance.

Although SW has been recognized as a primary source of nutrient in the Gulf of Maine (Bigelow 1927; Pastuszak et al. 1982; Schlitz and Cohen 1984; Ramp et al. 1985) and on the Scotian Shelf (Fournier et al. 1977; Houghton et al. 1978; Smith 1978), it was unclear whether observations of SW intrusions off southwest Nova Scotia should be considered anomalous or of more general significance (Denman and Herman 1978; Fournier et al. 1984). Our study indicates that in late spring, SSW and SW, as modified by thermal, convective, and mixing presses, play a major role in establishing the mean distribution of chemical and planktonic, as well as physical, oceanographic properties off southwest Nova Scotia; and the relative contribution of these water types is a major factor regulating interannual variability.

During the winter and spring of 1985, conditions generally favored the onshore movement of SW through upwelling and flow through the Northeast Channel, whereas the opposite conditions prevailed during that period in 1983 and 1984, when conditions favored enhanced flow of the Nova Scotia Current along the shelf. During the winter and spring of 1983–84, a positive atmospheric pressure anomaly generally prevailed over the North Atlantic, which reversed in 1985 (Fig. 10) (Trites and Drinkwater 1985, 1986; Drinkwater and Trites 1987). Since wind anomalies tend to follow positive isobar anomaly contours clockwise (and vice-versa), these conditions led to increased relatively warm onshore winds in the winter/spring of 1983–84 and cold offshore winds in 1985 over much of the area from the Gulf of Maine to the Grand Banks. This is confirmed by wind records from Yarmouth at the tip of southwest Nova Scotia and Sable Island on the Scotian Shelf (figure 8a,b in Smith 1989). Offshore winds are associated with increased inflow of SW through the Northeast Channel (Ramp et al. 1985). Yarmouth and Sable Island wind records also indicate that alongshore wind anomalies in winter and spring were generally from the northeast in 1983–84, which was associated with downwelling and enhanced inflow of the Nova Scotia Current into the region (figure 6 in Smith 1989). Wind anomalies in the winter and spring, 1985 were predominantly southwesterly, which enhanced upwelling and decreased alongshore flow of the shelf current (figure 6 in Smith 1989). Continuous salinity records indicate that these current anomalies were associated with the expected low salinity anomalies throughout much of 1983 and in spring, 1984, and with high salinity anomalies in the winter and spring of 1985 (figure 6 in Smith 1989).

On the other hand, currents and nutrient fluxes off southwest Nova Scotia in winter and spring did not appear related to the previous year's outflow from the St. Lawrence River, as hypothesized by Sutcliffe et al. (1976). As Smith (1989) noted, St. Lawrence outflows were anomalously low throughout 1982 and high in 1984, i.e. opposite to that expected if salinity anomalies off southwest Nova Scotia were driven by freshwater discharge, since there is a 9-mo transit time.

The influence of SW on plankton production off southwest Nova Scotia is analogous to that of the 'bourrelet froid' in tidally-energetic areas in the northeast Atlantic: a deep nutrient-rich layer formed in winter, whose subsequent mixing into the surface regulates productivity (Le Fevre 1986). However, the critical factor off southwest Nova Scotia appears to be the factors regulating shelf/slope exchange, i.e. winds and possibly warm-core rings (Ramp et al. 1985; Brooks 1987; Smith 1989).

Gadoid Recruitment

Recruitment to northwest Atlantic cod (*Gadus morhua*) stocks has been statistically associated with regional winter wind conditions established by a dominant pattern of North Atlantic atmospheric pressure anomalies similar to that seen in Fig. 10 (Koslow et al. 1987). However, Koslow et al. (1987) did not propose a mechanism linking recruitment to this pattern of prevailing winds, in part because so many factors, including sea surface temperature, freshwater discharge, and salinity, were correlated with winter wind conditions on the one hand and gadoid recruitment on the other.

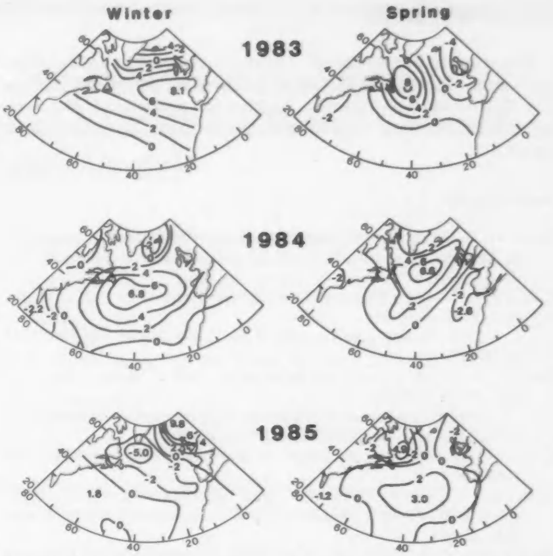

FIG. 10. Atmospheric pressure anomalies (in mbars) relative to 1951–80 over the North Atlantic during winter and spring, (a) 1983, (b) 1984, and (c) 1985 (from Trites and Drinkwater (1985, 1986) and Drinkwater and Trites (1987)).

We speculate that the relationship between atmospheric circulation, currents, and regional productivity may underlie correlations between recruitment to northwest Atlantic cod stocks and air pressure anomalies over the North Atlantic. Consistent with the large-scale coherence of recruitment to cod and haddock (*Melanogrammus aeglefinus*) stocks in the northwest Atlantic (Koslow 1984; Koslow et al. 1987), these relationships among atmospheric, physical and biological oceanographic processes may affect the area from the Grand Banks to the Gulf of Maine. The North Atlantic atmospheric pressure anomaly establishes coherent wind and sea surface temperature patterns over the shelf region from the Gulf of Maine to the Grand Banks (Loucks et al. 1986; Thompson et al. 1988). Upwelling and the flux of SW onto the Scotian Shelf as a whole appears to be driven by wind patterns similar to those that regulate nutrient dynamics off southwest Nova Scotia (Petrie and Smith 1977; Petrie 1983; Petrie et al. 1987). Furthermore, fluctuations in the flux of SW through the Northeast Channel influence the nutrient budget of Georges Bank and much of the Gulf of Maine, as well as the waters off southwest Nova Scotia (Bigelow 1927; Pastuszak et al. 1982; Schlitz and Cohen 1984; Ramp et al. 1985). Cod larval condition and growth appear related to zooplankton abundance in the field (Koslow et al. 1985; Suthers et al. 1989), but the links between environmental conditions, larval condition and growth, larval mortality, and subsequent recruitment must be tested.

Acknowledgments

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References

Anderson, E. 1974. Trophic interactions among ctenophores and copepods in St. Margaret's Bay, Nova Scotia. Ph.D. thesis, Dalhousie University, Halifax, N.S. 85 p.

Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. Fish. Bull. 40: 1–509.

1927. Physical oceanography of the Gulf of Maine. Fish. Bull. 40: 511–1027.

Brooks, D. A. 1985. Vernal circulation in the Gulf of Maine. J. Geophys. Res. 90: 4687–4705.

1987. The influence of warm-core rings on Slope Water entering the Gulf of Maine. J. Geophys. Res. 92: 8183–8196.

Cassie, R. M. 1968. Sample design. *In* Zooplankton sampling, UNESCO: 105–122.

Denman, K. L., and A. W. Herman. 1978. Space–time structure of a continental shelf ecosystem measured by a towed porpoising vehicle. J. Mar. Res. 36: 693–714.

Drinkwater, K. F., and R. W. Trites. 1987. An overview of environmental conditions in the northwest Atlantic in 1985. NAFO Sci. Coun. Studies 11: 23–35.

Fournier, R. O., J. Marra, R. Bohrer, and M. van Det. 1977. Plankton dynamics and nutrient enrichment of the Scotian Shelf. J. Fish. Res. Board Can. 34: 1004–1018.

Fournier, R. O., M. van Det, N. B. Hargreaves, J. S. Wilson, T. Clair, and R. Ernst. 1984. Physical factors controlling summer distribution of chlorophyll *a* off southwestern Nova Scotia. Limnol. Oceanogr. 29: 517–526.

Frank, K. T. 1986. Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 211–222.

Garrett, C. J. R., J. R. Keeley, and D. A. Greenberg. 1978. Tidal mixing versus thermal stratification in the Bay of Fundy and Gulf of Maine. Atmos.-Ocean 16: 403–423.

Greve, W. 1977. Interspecific interactions: the analysis of complex structures in carnivorous zooplankton populations. Helgolander. Wiss. Meeresunters 30: 83–91.

Hopkins, T. S., and N. Garfield III. 1979. Gulf of Maine Intermediate Water. J. Mar. Res. 37: 103–139.

Houghton, R. W., P. C. Smith, and R. O. Fournier. 1978. A simple model for cross-shelf mixing on the Scotian Shelf. J. Fish. Res. Board Can. 35: 414–421.

Judkins, D. C., C. D. Wirick, and W. E. Esaias. 1979. Composition, abundance, and distribution of zooplankton in the New York Bight, September 1974–September 1975. U.S. Fish. Bull. 77: 669–683.

Koslow, J. A. 1984. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 41: 1722–1729.

Koslow, J. A., S. Brault, J. Dugas, R. O. Fournier, and P. Hughes. 1985. Condition of larval cod (*Gadus morhua*) off southwest Nova Scotia in 1983 in relation to plankton abundance and temperature. Mar. Biol. 86: 113–121.

Koslow, J. A., K. R. Thompson, W. Silvert. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Can. J. Fish. Aquat. Sci. 44: 26–39.

Lauzier, L. M. 1967. Bottom residual drift on the continental shelf area of the Canadian Atlantic coast. J. Fish. Res. Board Can. 24: 1845–1858.

Le Fevre, J. 1986. Aspects of the biology of frontal systems. Adv. Mar. Biol. 23: 163–299.

Loucks, R. H., K. R. Thompson, and R. W. Trites. 1986. Sea surface temperature in the northwest Atlantic — space and time scales, spectra and spatially smoothed fields. Can. Tech. Rep. Fish. Aquat. Sci. 1430: 80 p.

Milliken, G. W., and D. E. Johnson. 1984. Analysis of messy data. Lifetime Learning Publ. Belmont, Ca.

Milne, W. R. 1984. Distribution and feeding ecology of ctenophores in the Bay of Fundy. M.Sc. thesis, University of Guelph, Guelph, Ontario. 176 p.

Mountain, D. G., and P. F. Jessen. 1987. Bottom waters of the Gulf of Maine, 1978–1983. J. Mar. Res. 45: 319–345.

Norusis, M. J. 1988. SPSS/PC+ Advanced Statistics V2.0. SPSS, Inc. Chicago, Illinois.

Pastuszak, M., W. R. Wright, and D. Patanjo. 1982. One year of nutrient distribution in the Georges Bank region in relation to hydrography, 1975–1976. J. Mar. Res. 40 (Suppl.): 525–542.

Perry, R. I., P. C. F. Hurley, P. C. Smith, J. A. Koslow, and R. O. Fournier. 1989. Modelling the initiation of spring phytoplankton blooms: a synthesis of physical and biological interannual variability off southwest Nova Scotia, 1983–85. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): (This issue).

Petrie, B. D. 1983. Current response at the shelf break to transient wind forcing. J. Geophys. Res. 88: 9567–9578.

Petrie, B., and P. C. Smith. 1977. Low-frequency motions on the Scotian shelf and slope. Atmosphere 15: 117–140.

Petrie, B., B. J. Topliss, and D. G. Wright. 1987. Coastal upwelling and eddy development off Nova Scotia. J. Geophys. Res. 29: 12 979–12 991.

Ramp, S. R., R. J. Schlitz, and W. R. Wright. 1985. The deep flow through the northeast channel, Gulf of Maine. J. Phys. Ocean. 15: 1790–1808.

Schlitz, R. J., and E. B. Cohen. 1984. A nitrogen budget for the Gulf of Maine and Georges Bank. Biol. Ocean. 3: 203–222.

Smith, P. C. 1978. Low-frequency fluxes of momentum, heat, salt, and nutrients at the edge of the Scotian shelf. J. Geophys. Res. 83: 4079–4096.

1983. Mean and seasonal circulation off southwest Nova Scotia. J. Phys. Ocean. 13: 1034–1054.

1989. Seasonal and interannual variability off southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): (This issue).

Strickland, J. D. H., and T. R. Parsons. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167: 293 p.

Sutcliffe, W. H., Jr., R. H. Loucks, and K. F. Drinkwater. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33: 98–115.

Suthers, I. M., K. T. Frank, and S. E. Campana. 1989. Spatial comparison of recent growth in postlarval cod (*Gadus morhua*) off southwestern Nova Scotia: inferior growth in a presumed nursery area. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): (This issue).

Thompson, K. R., R. H. Loucks, and R. W. Trites. 1988. Sea surface temperature variability in the shelf–slope region of the northwest Atlantic. Atmos.-Ocean 26: 282–299.

Tremblay, M. J., and J. C. Roff. 1983. Community gradients in the Scotian shelf zooplankton. Can. J. Fish. Aquat. Sci. 40: 598–611.

Trites, R. W., and K. F. Drinkwater. 1985. Overview of environmental conditions in the northwest Atlantic in 1983. NAFO Sci. Coun. Studies 8: 7–20.

1986. Overview of environmental conditions in the northwest Atlantic in 1984. NAFO Sci. Coun. Studies 10: 21–34.

Stage Dependent Vertical Distribution of Haddock (*Melanogrammus aeglefinus*) Eggs in a Stratified Water Column: Observations and Model[1]

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The depth distribution of four development stages of haddock (*Melanogrammus aeglefinus*) eggs was measured during May 1984 in a continuously stratified water column over Browns Bank. The egg profile varied with development. Early stage eggs were most concentrated near the sea surface whereas late stage eggs were distributed uniformly over depth or had a subsurface maximum. In order to explain the shape of these profiles a one-dimensional (vertical) advection–diffusion model including density stratification was used. Model egg profiles compared favourably with observed profiles and indicate that a large proportion (>30%) of haddock eggs are below the Ekman depth (δ_e). This proportion increases as the eggs develop. For example more than 50% of the stage III and IV eggs are below δ_e. Surface drift bottles and other indicators of the very near surface wind-driven transport would appear to be poor indicators of egg transport in haddock and possibly several other species, such as Atlantic cod (*Gadus morhua*) and mackerel (*Scomber scombrus*).

Nous avons établi la distribution suivant la profondeur des oeufs d'églefin (*Melanogrammus aeglefinus*) à quatre de leurs stades de développement au cours du mois de mai 1984 dans une colonne d'eau régulièrement stratifiée sur le banc Browns. Le profil de distribution des oeufs était fonction de leur stade de développement. À leur premier stade, les oeufs étaient surtout concentrés près de la surface de la mer tandis qu'à leur stade tardif, ils étaient distribués de façon uniforme sur toute la colonne d'eau ou jusqu'à une certaine profondeur. Afin d'expliquer la forme de ces profils, nous avons utilisé un modèle unidimensionnel (vertical) d'advection et de diffusion prenant en compte la stratification suivant la densité. Les profils de distribution des oeufs obtenus avec le modèle ont donné des résultats similaires aux profils observés et montrent qu'une grande proportion (>30 %) des oeufs d'églefin se trouvent sous la profondeur d'Ekman (δ_e). Plus les oeufs sont développés, plus cette proportion augmente. Par exemple, plus de 50 % des oeufs des stades III et IV se trouvaient sous la profondeur d'Ekman. L'utilisation de bouteilles dérivant à la surface et d'autres indicateurs du transport dû au vent tout près de la surface semble être inefficace pour évaluer le transport des oeufs d'églefin et peut-être de plusieurs autres espèces, comme la morue franche (*Gadus morhua*) et le maquereau (*Scomber scombrus*).

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It is generally believed that the vertical distribution of pelagic organisms plays an important role in determining the rate and direction of their horizontal displacement and their interactions with prey and predators. A considerable amount of effort has, therefore, been devoted to describing the vertical distribution of aquatic organisms, including fish larvae. However, relatively few studies have focused on fish eggs despite early suggestions that variation in egg dispersal may affect year-class size (Hjort 1914, 1926).

Empirical studies of the relationship between water transport and year-class size have often assumed the eggs and larvae are near the surface where wind-driven Ekman transport can influence their displacement. However, the vertical distribution and specific gravity of fish eggs may vary between species and throughout development (Jacobsen and Johansen 1908; Tables 1 and 2) and during wind events eggs may be mixed below the surface (Fish 1928). The quantitative influence of these changes on egg transport are not well known.

The spawning grounds of haddock are often located near the edge of continental shelves (Walford 1938; Saville 1956, 1959; Colton and Temple 1961; O'Boyle et al. 1984; Smith and Morse

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TABLE 1. Studies examining the vertical distribution of developing pelagic fish eggs.

Species	Location	Comments	Source
Sprat	English Channel	Vertical distribution is similar throughout development	a
Pilchard	English Channel	Vertical distribution is similar throughout development	a
Mackerel	New England	Eggs become less concentrated at the surface as they develop	b
Jack mackerel	California	Middle and late stage eggs are more concentrated near the surface than recently spawned eggs	c
Cod	Nova Scotia	Eggs become relatively less concentrated at the surface as they near the time of hatching	d
	Austnesfjorden, Norway	Newly fertilized eggs become more concentrated toward the surface as they develop	e
Haddock	Georges Bank	All egg stages, from newly spawned to nearly hatching, have a similar vertical distribution	f
	Georges Bank and Gulf of Maine	Early and late stage eggs have very similar distributions	g
Cod/haddock	Iceland	All egg stages have highest concentrations at the surface, however, the rate at which the concentrations decrease with depth decreases with egg development	h
Plaice	Southern North Sea	Vertical distribution is similar throughout development, winds generally greater than 10 m/s	i
		Earlier developmental stages closer to the surface than older stages, winds very clam	j
Halibut	Malangen, Norway	Vertical distribution of all egg stages similar	k,l
	Andfjord and Soroysund, Norway	Older stage eggs found deeper in the water column than younger stages	l
California sardine	California	1–2 d old eggs more concentrated near the suface than newly spawned, 2–3 or 3–4 d old eggs	c

[a] Coombs et al. 1984.
[b] Sette 1943.
[c] Ahlstrom 1959.
[d] McKenzie 1940.
[e] Solemdal and Sundby 1981.
[f] Walford 1938.
[g] Colton 1965.
[h] Fridgeirsson 1984.
[i] Coombs et al. 1981.
[j] Pommeranz 1973 as cited in Coombs et al. 1981.
[k] Haug et al. 1984.
[l] Haug et al. 1986.

1985; Koslow et al. 1985). There has, therefore, been much interest in whether the eggs are transported off the continental shelf or retained over it and whether interannual variation in the transport, particularly wind driven transport, is a major cause of recruitment variation. Haddock (*Melanogrammus aeglefinus*) has therefore been the focus of several wind-recruitment correlation studies (Carruthers 1938; Carruthers et al. 1951; Chase 1955).

Spawning of haddock occurs near the bottom (Needler 1931; Walford 1938) during the spring when the water column is beginning to stratify; the eggs subsequently float toward the surface. Walford (1938) and Colton (1965) indicated that 80% or more of the eggs on Georges Bank were found within the top 55 m. These workers also claimed that ontogenetic variation in the vertical distribution pattern did not occur. However, they used sampling methods that may not have resolved ontogenetic variation because of the broad depth intervals sampled and the coarse egg staging system employed.

Laboratory experiments provide evidence that ontogenetic variation in the depth distribution of haddock eggs does occur. Eggs, reared in sea water of constant density, change specific gravity with development. Early stage haddock eggs tend to adjust their specific gravity toward that of the ambient sea water (Bigelow and Welch 1925; Walford 1938). Egg specific gravity appears to decrease after fertilization to a minimum during gastrulation, and thereafter increases until hatching (Wheeler and Miller 1960; Moksness and Torstensen 1985). If such changes were to occur in the field, stage-specific variation in the vertical distribution would be expected, particularly in regions where the water column is weakly stratified and vertical mixing rates are relatively low.

Field surveys have usually shown that the horizontal displacements of haddock eggs or larvae are small relative to expectations based on the displacement of surface drift bottles and wind-based indices of the near surface circulation (Saville 1959; Koslow et al. 1985; references in Smith and Morse 1985).

TABLE 2. Ontogenetic variation in the density of live fish eggs. Abbreviations refer to the source of the eggs used in density determinations (AF = artificially fertilized, PNT = plankton net tows, MSC = maintained and spawned naturally in captivity).

Species	Location	Comments	Source
Sprat	English Channel	Density increases continuously with development, PNT	[a]
	Flodevigen, Norway	Decrease in density with development, MSC	[b]
	Frierfjord, Norway	Maximum density during early egg development, PNT	[b]
Pilchard	English Channel	Density increases near the end of the egg stage, PNT	[a]
Mackerel	Celtic Plateau	Density decreases continuously with development, AF	[c]
	Plymouth, England	Density increases with development, PNT	[a]
Cod	Lofoten, Norway	Density increases continuously throughout development, AF	[d]
Haddock	Gulf of Maine	Density minimum midway through egg stage	[e]
	Unspecified	Density minimum during gastrulation	[f]
Plaice	Southern North Sea	No trend in density with development	[g]
Halibut	Malangen and Soroysund, Norway	No trend in density with development	[h]
	Malangen, Soroysund and Andfjord, Norway	Density increases near the end of the egg stage, PNT	[i]

[a] Coombs et al. 1985.
[b] Moksness and Torstensen 1985.
[c] Coombs 1981.
[d] Sundnes et al. 1965.
[e] Wheeler and Miller 1960.
[f] Moksness and Selvik 1984 as cited in Moksness and Torstensen 1985.
[g] Coombs et al. 1981.
[h] Haug et al. 1984.
[i] Haug et al. 1986.

The discrepancy may stem from the assumption that the eggs and larvae are concentrated near the surface (Colton and Temple 1961) because the displacements often compare more favourably with expectations based on the mid-depth circulation (e.g. Georges Bank, Smith and Morse 1985).

One of the major objectives of the Southwest Nova Scotia Fisheries Ecology Program has been to gain a better understanding of the mechanisms underlying the displacement patterns of haddock eggs and larvae originating from Browns Bank. To achieve this, field surveys were conducted to describe the distribution of the early life stages and models have been developed to assist in quantifying the physical forces controlling such distributions. This paper presents observations on the vertical distribution of haddock eggs in relation to the depth of the surface wind-driven layer. We test the hypothesis that the vertical distribution varies ontogenetically, and present a vertical advection–diffusion model of egg concentration.

Materials and Methods

Sampling Area and Procedures

The vertical distribution of haddock eggs was derived from samples collected at 13 stations on the eastern cap of Browns Bank during a 3–7 May 1984 cruise aboard the *C.S.S. Dawson*. The time and location of sampling was based on the fact that the peak spawning period for haddock occurs during April and May on Browns Bank (Page and Frank 1989).

At each station ichthyoplankton samples were collected at seven discrete depths within the interval of 5–65 m depth. The water depth in the sampling area varied between 90 and 100 m. All samples were collected with a mini-BIONESS using 333-μm mesh nets with a mouth area of 0.25 m^2. BIONESS tows were made in a constant direction for 10 min at each depth at an average speed of 1.5 m/s. Each sample therefore represented a spatial average taken over a horizontal distance of approximately 900 m. Flow meters fixed to the outside and inside of the mini-BIONESS provided a continuous record of the volumes of water being filtered and the filtration efficiency. A more detailed description of the mini-BIONESS system and its mode of operation is given by Frank (1986).

Temperatures and salinities were measured continuously throughout each tow with an Applied Microsystems CTD (conductivity, temperature, depth) attached to the BIONESS. Water density was calculated continuously using each discrete temperature and salinity measurement. Mean values (time average over approximately 10 min) for each tow and discrete sampling depth were then calculated. These mean values were used in the present analyses.

Once on deck, the plankton nets were thoroughly washed and the contents of each cod-end were passed through a 4-mm mesh sieve to remove the macrozooplankton, primarily gelatinous zooplankton and euphausids. The smaller size fraction (<4 mm) was preserved in a solution of 4% formalin (buffered with Borax) and sea water for subsequent sorting and enumeration.

In the laboratory all fish eggs were identified and classified into four developmental stages described in Page and Frank (1989). Because haddock eggs cannot be distinguished from witch flounder (*Glyptocephalus cynoglossus*) until stage III or from Atlantic cod (*Gadus morhua*) until stage IV, the abundances reported here for stages I and II include all three species and those for stage III include cod and haddock. Stage IV eggs include only haddock. Because the majority of the stage IV cod–haddock–witch eggs collected were haddock (81.1% haddock, 11.1% cod, and 7.8% witch flounder), all egg stages were assumed to be dominated by haddock.

For the cod–haddock–witch complex the diameters of the preserved eggs ranged mainly between 1.4 and 1.6 mm. The ratio of the preserved to fresh egg diameter is 0.98 (Hislop and Bell 1987) and the eggs were assigned a constant diameter of 1.5 mm.

Water velocity measurements were made so that a scaling of the advection–diffusion equations could be carried out to help isolate the important forcing terms. The horizontal components (north–south and east–west) of water velocity were obtained for the depth range 16.8 to 74.4 m during each mini-BIONESS tow with an Ametek Straza Doppler acoustic profiling system mounted in the hull of the *C.S.S. Dawson*. This system does not provide accurate estimates within the bottom 20% of the water column nor within a few metres of the transducer.

Results

Vertical Distribution of Haddock Eggs

The majority of the stage I (> 80%), II (> 80%), and III (> 50%) eggs were within the top 20 m of the water column and their concentration decreased exponentially with depth (Table 3). Only 30% of the stage IV eggs were within the top 20 m (Table 3) and it is apparent that their distribution is consistent with a more uniform depth distribution or possibly a subsurface maximum. The stage IV center-of-mass (31 m) is two to three times deeper than that of the stage I and II eggs and 1.5 times that of the stage III eggs.

These results, with the exception of a subsurface maximum in the stage IV eggs, are supported by linear regression analyses of the natural logarithm transformed mean and median egg concentrations versus depth (Table 4). The regressions were calculated once using all nine sample depths and again using only the seven most frequently sampled depths. All of the stage I, II, and III regressions were statistically significant (*F*-test; Zar 1974). Only the mean concentrations were used in the stage IV regressions since the medians were equal to zero for all depths. These regressions were not statistically significant. The mean concentration was greater than zero (*t*-test, $p<0.025$).

Comparisons of the stage I, II, and III regression slopes using analysis of covariance and the Newman-Keuls multiple range test (Table 4; Zar 1974) indicated that the slope of the stage I eggs was indistinguishable from stage II eggs, and the slope of the stage II eggs was different from the slope of the stage III eggs (Fig. 1). The apparent maxima in the median egg concentrations at 25 and 55 m are associated with the small number of samples ($n=7$) taken at this depth relative to that taken at the other depths ($n=21$–28).

The age of each of each egg stage was estimated from age–temperature relationships (Page and Frank 1989) using the mean water temperature in the upper 35 m (3.5°C). This yielded ages of 2.4, 6.9, 10.8, and 15.2 d for stages I through IV, respectively.

Physical Properties of the Water Column

The temperatures ranged from 3.3 to 4.1°C with a minimum at mid-depth, salinity increased with depth from 32.0 at 5 m to 33.0 at 65 m, and the water density (sigma-*t*) increased from 25.4 at 5 m to 26.1 at 65 m (Fig. 2). The variability in temperature and salinity increased below 40 m. The apparent local minimum in temperature, salinity, and sigma-*t* at 50 m is associated with the small number ($n=7$) of observations at this depth. Collectively these observations suggest the water column was not well mixed.

The velocity observations were dominated by the M_2 tidal cycle. To determine the mean velocity, the tidal amplitude, and phase of the current as a function of depth, a curve of the form,

$$(1)\quad V(z) = \bar{V}(z) + A(z)\sin\left[\frac{2\pi t}{T} + P(z)\right] + e(z),$$

was fitted to the north–south and east–west velocity series from each depth (Table 5). In this equation $V(z)$ represents a given velocity component at depth z, $\bar{V}(z)$ the depth dependent mean velocity, $A(z)$ the depth dependent amplitude, $P(z)$ the depth dependent phase and T is the M_2 tidal period (12.4 h). In all cases the regression explained a large proportion of the variance, indicating the tides were the major cause of the current variability. The tidal amplitude varied little with depth, except perhaps near the bottom. The phases increased below 50 m (Table 5). The mean flow at all depths was generally toward the southwest with the magnitude decreasing with depth from 0.10 m/s at 16.8 m to 0.035 m/s at 74.4 m.

The observed mean advection rate at 16.8 m, (10cm/s = 8.6 km/d), coupled with the assumption of a passive egg drift and no velocity shear above this depth, indicates the haddock eggs were advected through the sampling area (grid diameter is approximately 40 km) within about 5 d, a time similar to the duration of the sampling period (5 d) and the age of the stage II eggs (6.9 d). The major axes of the tidal excursion ellipses are approximately 11.8 km, one-quarter the diameter of the sampling grid.

Model of Egg Vertical Distribution

The general equation for describing the rate of change in the concentration of a nonconservative substance, such as fish eggs, is according to Nihoul (1975)

$$(2)\quad \frac{\partial C}{\partial t} + \frac{\partial[(u+U)C]}{\partial x} + \frac{\partial[(v+V)C]}{\partial y} + \frac{\partial[(w+W)C]}{\partial z} = \frac{\partial}{\partial x}\left[K_x\frac{\partial C}{\partial x}\right] + \frac{\partial}{\partial y}\left[K_y\frac{\partial C}{\partial y}\right] + \frac{\partial}{\partial z}\left[K_z\frac{\partial C}{\partial z}\right] + \text{sources} + \text{sinks},$$

where $C = C(x, y, z, t)$ is the spatially- and temporally-dependent concentration of the substance, x and y denote the horizontal position, z denotes the vertical position (negative below the undisturbed sea surface), t denotes the time, u, v, and w are the spatial components of the water velocity, U, V, and W are the spatial components of the velocity generated by the substance (settling velocity, swimming velocity, etc.), and K_x, K_y, and K_z are the turbulent eddy diffusivities.

TABLE 3. Stage dependent depth distribution of haddock eggs, collected over Browns Bank in May of 1984. CV = standard deviation/mean; Cum% = cumulative percent of eggs within and above the sample depth; Sk = skewness, CN = centroid).

Stage	Depth	Total number of samples taken	Number of samples with eggs	No. of eggs per 100 m^3		CV	Cum. %	Median No. of eggs per 100 m^3	Sk
				Mean	SD				
I	5	22	22	246.7	(497.1)	2.0	54.4	55.0	1.16
	10	25	25	96.8	(124.3)	1.3	75.8	57.1	0.96
	20	27	27	28.7	(19.3)	0.7	82.2	25.4	0.51
	25	7	7	26.3	(19.9)	0.8	88.0	20.5	0.87
	35	28	27	15.5	(14.1)	0.9	92.5	11.1	0.94
	45	21	21	10.4	(12.4)	1.2	94.8	6.0	1.06
	50	7	7	16. 2	(19.1)	1.2	97.2	9.6	1.04
	55	21	21	6.4	(5.3)	0.8	98.6	4.1	1.30
	65	28	28	4.7	(6.2)	1.3	100.0	2.6	1.02
Total (eggs/m^2)				3398.4				1445.4	
CN (m)				13.1				17.8	
II	5	22	20	63.8	(177.3)	2.8	50.9	10.9	0.90
	10	25	24	28.9	(39.0)	1.3	74.0	10.5	1.41
	20	27	23	13.1	(20.0)	1.5	84.5	4.5	1.29
	25	7	5	11.0	(20.0)	0.8	93.3	15.5	−1.44
	35	28	24	4.3	(9.4)	1.3	97.9	3.2	0.60
	45	21	14	0.9	(5.5)	1.3	98.6	0.5	1.00
	50	7	5	1.0	(1.2)	1.0	99.2	1.0	0.00
	55	21	14	0.5	(1.0)	1.1	99.6	0.5	0.00
	65	28	11	0.4	(0.6)	1.6	100.0	0.0	2.00
					(0.6)				
Total (eggs/m^2)				940.3				355.2	
CN (m)				11.6				18.2	
III	5	22	14	8.8	(10.9)	1.2	20.2	3.6	1.43
	10	25	19	7.4	(15.1)	2.0	37.3	3.6	0.75
	20	27	19	6.3	(12.2)	2.0	51.7	1.9	1.08
	25	7	5	11.2	(13.4)	1.2	77.4	3.9	1.63
	35	28	15	4.9	(9.0)	1.8	92.3	0.6	1.43
	45	21	10	0.7	(1.2)	1.6	94.0	0.0	1.75
	50	7	3	2.4	(3.0)	1.3	97.6	0.0	2.40
	55	21	8	0.7	(2.0)	2.6	99.3	0.0	1.05
	65	28	8	0.2	(0.5)	2.2	100.0	0.0	1.20
Total (eggs/m^2)				327.5				104.0	
CN (m)				21.1				15.6	
IV	5	22	4	0.2	(0.5)	2.7	9.8	0.0	1.20
	10	25	3	0.1	(0.3)	3.1	15.2	0.0	1.00
	20	27	5	0.3	(1.0)	3.2	29.8	0.0	0.90
	25	7	1	0.1	(0.2)	2.6	34.2	0.0	1.50
	35	28	7	0.8	(1.8)	2.4	84.4	0.0	1.33
	45	21	1	0.0	(0.1)	4.6	85.3	0.0	0.00
	50	7	2	0.2	(0.5)	1.9	93.2	0.0	1.20
	55	21	3	0.1	(0.2)	2.5	96.1	0.0	1.50
	65	28	3	0.1	(0.2)	3.0	100.0.	0.0	1.50
Total (eggs/m^2)				15.4				0.0	
CN (m)				31.0				undefined	
Total	5	22	22	319.6	(648.8)	2.0	51.2	79.8	1.11
	10	25	25	133.3	(156.1)	1.2	72.6	72.9	1.16
	20	27	27	48.4	(37.7)	0.8	80.3	35.1	1.06
	25	7	7	48.7	(21.1)	0.4	88.1	59.1	−1.48
	35	28	28	25.5	(19.8)	0.8	93.6	20.0	0.83
	45	21	21	12.1	(12.2)	1.0	95.5	7.6	1.11
	50	7	7	19.8	(18.2)	0.9	97.6	13.4	1.05
	55	21	21	7.7	(6.3)	0.8	98.8	5.7	0.95
	65	28	28	5.4	(6.6)	1.2	100.0	3.2	1.00
Total (eggs/m^2)				4681.7				2250.5	
CN (m)				13.4				18.7	

TABLE 4. Stage specific linear regressions of egg concentration ($\mathrm{Ln}(C(z)+1)$) on depth (z). (R^2 is the coefficient of determination).

Egg stage	Intercept	Slope	n	R^2	Ho: slope = 0
All nine depths					
Mean					
I	5.051	−0.054	9	0.87	Rej. $p<0.0005$
II	4.113	−0.066	9	0.95	Rej. $p<0.0005$
III	2.744	0.037	9	0.80	Rej. $p<0.0025$
IV	0.221	−0.001	9	0.02	Acc. $p>0.25$
Ho: slope I = slope II = slope III					Rej. $p<0.025$
Ho: slope I = slope II					Acc. $p>0.20$
Ho: slope I = slope III					Acc. $p>0.20$
Ho: slope II = slope III					Rej. $p<0.01$
Median					
I	4.297	−0.047	9	0.96	Rej. $p<0.0005$
II	2.960	−0.046	9	0.84	Rej. $p<0.001$
III	1.801	−0.032	9	0.85	Rej. $p<0.0005$
Ho: slope I = slope II = slope III					Acc. $p>0.25$
Only seven depths					
Mean					
I	5.159	−0.058	7	0.91	Rej. $p<0.001$
II	4.103	−0.066	7	0.95	Rej. $p<0.0005$
III	2.594	−0.037	7	0.91	Rej. $p<0.001$
IV	0.243	−0.002	7	0.04	Acc. $p>0.25$
Ho: slope I = slope II = slope III					Rej. $p<0.05$
Ho: slope I = slope II					Acc. $p>0.50$
Ho: slope I = slope III					Acc. $p>0.10$
Ho: slope II = slope III					Rej. $p<0.025$
Median					
I	4.324	−0.049	7	0.98	Rej. $p<0.0005$
II	2.728	−0.043	7	0.96	Rej. $p<0.0005$
III	1.655	−0.030	7	0.92	Rej. $p<0.001$
Ho: slope I = slope II = slope III					Rej. $p<0.005$
Ho: slope I = slope II					Acc. $p>0.20$
Ho: slope I = slope III					Acc. $p<0.005$
Ho: slope II = slope III					Rej. $0.1>p>0.05$

In the present context C is the concentration of fish eggs, and W is the terminal velocity of the egg (velocity at which drag balances gravity). The source term is assumed to be zero (eggs are introduced as initial conditions) and the sink term is considered to be the loss of eggs caused by natural mortality. This is represented as $-MC$, where M is the rate of egg mortality.

When it is assumed the vertical water velocity is zero and that horizontal velocities or gradients in the egg concentration are sufficiently small as to make the horizontal advection and diffusion terms negligible, equation (2) reduces to

$$(3)\quad \frac{\partial C}{\partial t} + \frac{\partial (WC)}{\partial z} = \frac{\partial}{\partial z}\left[K_z \frac{\partial C}{\partial z}\right] - MC.$$

This equation states that the rate of change in egg concentration is due to the divergence of the vertical flux of the eggs and the loss due to natural mortality. The vertical flux is $WC - K_z \partial C/\partial z$.

Typical values for W, K_z, and M are 10^{-3}m/s (Sundby 1983; Wheeler and Miller 1963), 10^{-2} m^2/s (Sundby 1983; Loder et al. 1988), and 0.1/d (Dahlberg 1979), respectively. A reasonable vertical scale for the distribution of buoyant eggs (Z) is 10 m (Sundby 1983; Fridgeirsson 1984). These values indicate the mortality time scale ($1/M = 10^6$ s $= 10$ d) is long relative to both the advective ($Z/W = 10^4$s $\simeq 3$ h) and diffusive ($Z^2/K_z = 10^4$s $\simeq 3$ h) time scales. The mortality term will therefore also be neglected.

Although this scaling assumes K_z is constant over time, K_z is in reality variable (e.g. Loder et al. 1988). However, much of the variation occurs on time scales that are long relative to the advective and diffusive time scales therefore making it reasonable to assume a constant K_z in our model. Furthermore, as long as the duration of a specific egg stage is longer than the advective and diffusive time scales it is also reasonable to assume a steady-state profile which satisfies

$$(4)\quad \frac{\partial}{\partial z}\left(WC - K_z \frac{\partial C}{\partial z}\right) = 0.$$

When the concentration is assumed to be zero at great depth the solution to equation (4) is

$$(5)\quad C(z) = C_0 \exp\left(-\int_z^0 W/K_z\, dz\right),$$

where C_o is the egg concentration at the surface ($z=0$).

If both W and K_z are assumed to be independent of depth, the concentration profile decays exponentially with an e-folding scale of K_z/W. Sundby (1983) has shown that this solution agrees well with observed distributions of early stage cod, mackerel, and American plaice (*Hippoglossoides platessoids*) eggs within the well-mixed surface layer. This solution, however, does not allow a subsurface maximum in $C(z)$. However, the concentration profiles of the stage IV haddock eggs reported here, as well as the egg profiles of several other fish species (e.g. pilchard, Coombs et al. 1985; halibut, Haug et al. 1984, 1986) have subsurface maxima when the water column is stratified. We have therefore extended Sundby's (1983) solution by deriving a solution for the case of a continuously stratified water column. We have done this by parameterizing the terminal velocity of the egg as a function of the depth dependent water density. The terminal velocity (W) can be estimated using

$$(6a)\quad W = \frac{d^2 g\,(\rho_w - \rho_e)}{18\nu} \qquad Re<0.5$$

$$(6b)\quad W = \frac{K_t d_0 (\rho_w - \rho_e)^{2/3}}{\nu^{1/3}} \qquad 0.5<Re<5,$$

where equation (6a) is Stokes' equation for spherical particles (most fish eggs are spheres) and (6b) is Dallavalle's modified Stokes equation (Sundby 1983). In these equations ν is the molecular viscosity of sea water (1.61×10^{-3} kg·m^{-1}·s^{-1} at 5°C and salinity 35; Dorsey 1940), ρ_w is the density of the water, ρ_e is the density of the egg, g is the acceleration due to gravity, K_t is a constant which has a value of approximately 19 (c.g.s. units; Sundby 1983), d_o is an artificial egg diameter given by $d_o = d - 0.4D$, d is the true egg diameter, D is the egg diameter above which the Stoke's equation no longer applies and Re is the Reynolds Number defined by $\rho_w WD/\nu$.

The diameter of a haddock egg is approximately 1.5 mm and the experimentally measured terminal velocity is of order 10^{-3}m/s (Wheeler and Miller 1960). These values are not unlike those of other species (Sundby 1983). The Reynolds number is therefore of order one and Dallavalle's relationship gives the

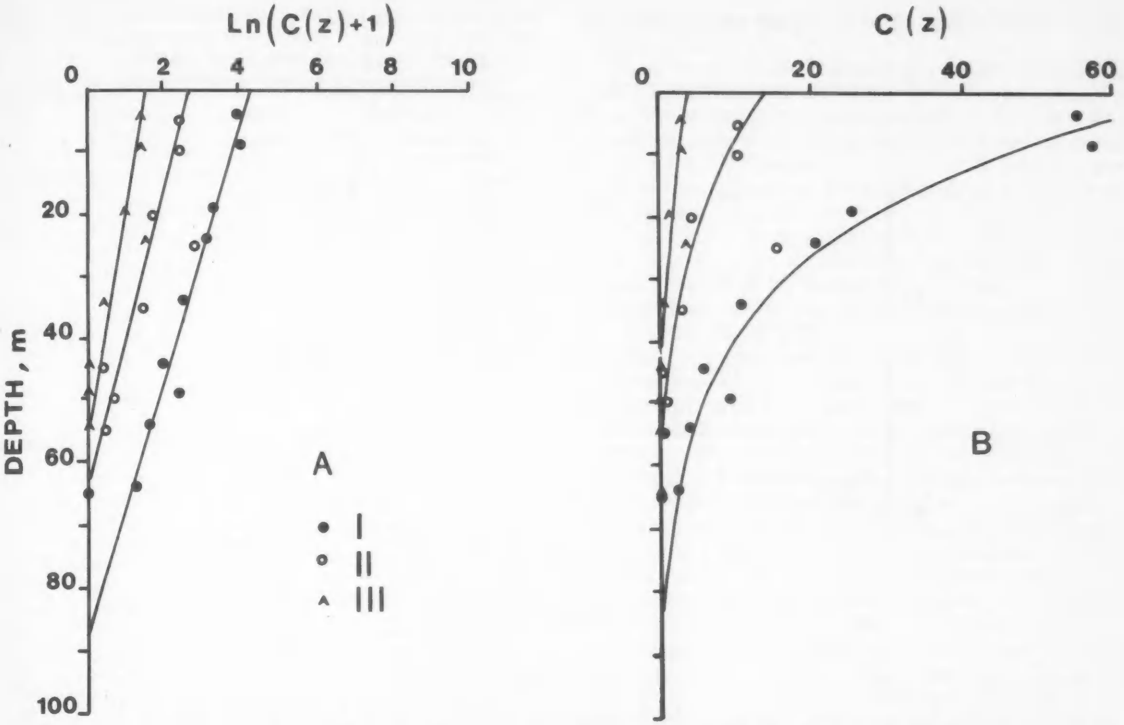

FIG. 1. Plots of the regression curves fit to the median egg concentrations of stages I, II, and III. (A) Logarithmic plot, (B) Arithmetic plot. The concentration of eggs at each depth ($C(z)$) has units of number per 100 cubic metres.

best estimate of the terminal velocity. However, Stokes' equation has been used because it is more amenable to analytical manipulations. A 25% error in terminal velocity estimates is associated with making this choice.

Assuming that the water density (ρ_w) increases linearly with depth

$$(7)\quad \rho_w(z) = \rho_o + (d\rho_w/dz)z$$

such that ρ_o is the water density at $z=0$ and $d\rho_w/dz$ is the vertical density gradient, the Stokes' terminal velocity relationship becomes

$$(8)\quad W(z) = \frac{d^2\, g\, (\rho_0 - \rho_e)}{18\nu} + \frac{d^2\, g\, (d\rho_w/dz)\, z}{18\nu}$$

Substitution of equation (8) into equation (5), leads to

$$(9)\quad C(z) = Co \exp\left(\frac{W_0}{K_z} z + \frac{d^2 g\, d\rho_w/dz}{18\nu K_z}\, \frac{z^2}{2}\right)$$

where W_0 is the terminal velocity of the egg at $z = 0$,

$$W_0 = \frac{d^2\, g\, (\rho_0 - \rho_e)}{18\nu}\ .$$

Inspection of equation (9) indicates there are three general cases.

Case (1) $\rho_e = \rho_o$: The egg is neutrally buoyant at the sea surface ($W_o=0$) and positively buoyant below. The maximum egg concentration is at the surface and decreases monotonically with depth. The profile is a gaussian curve centered at the surface (Fig. 3b):

$$(10)\quad C(z) = Co \exp\left(-\frac{1}{2}\left[\frac{z}{\delta_1}\right]^2\right)$$

where δ_1 is the vertical scale (or standard deviation) of the depth distribution given by

$$\delta_1 = \left(-\frac{18\nu K_z}{d^2 g \partial\rho_w/\partial z}\right)^{1/2}$$

Case (2) $\rho_e<\rho_o$: The egg is positively buoyant at the surface ($W_o>0$). Again the maximum egg concentration is at the sea surface. However, now the profile is given by

$$(11)\quad C(z) = Co \exp\left(\frac{z}{\delta_2} - \frac{1}{2}\left[\frac{z}{\delta_1}\right]^2\right)$$

where δ_2 is another e-folding scale defined by

$$\delta_2 = |K_z/W_0|.$$

Typical profiles of this type are shown in Fig. 3a.

Case (3) $\rho_e>\rho_o$: The egg is negatively buoyant (sinking) at the surface ($W_o<0$). This is the most interesting case because we can now describe, in contrast to Sundby (1983), a subsurface maximum. The egg concentration increases with depth to a subsurface maximum at $z=z_n$, where z_n is the depth of neutral buoyancy defined by $z_n = (\rho_e-\rho_o)/\partial\rho_w/\partial z$ (Fig. 3b). The profile is given by

$$(12)\quad C(z) = Co \exp\left(-\frac{z}{\delta_2} - \frac{1}{2}\left[\frac{z}{\delta_1}\right]^2\right)\ .$$

Note that for a homogeneous water column $\partial\rho/\partial z = 0$ and equation (9) reduces to

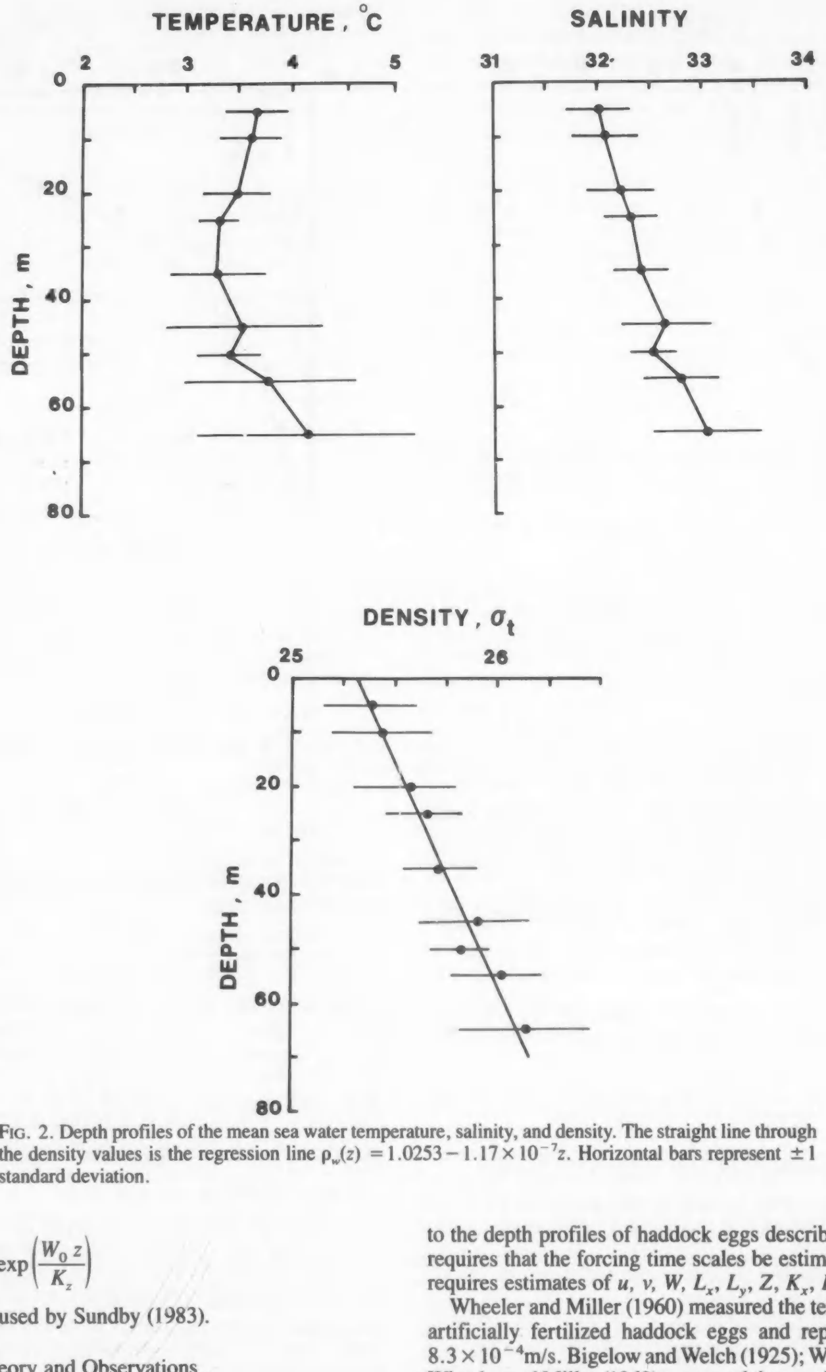

FIG. 2. Depth profiles of the mean sea water temperature, salinity, and density. The straight line through the density values is the regression line $\rho_w(z) = 1.0253 - 1.17 \times 10^{-7} z$. Horizontal bars represent ±1 standard deviation.

$$(13) \quad C(z) = Co \exp\left(\frac{W_0 z}{K_z}\right)$$

which is the form used by Sundby (1983).

Comparison of Theory and Observations

The steady-state theory developed above assumes the mortality, horizontal advection, and horizontal diffusion time scales are small relative to the time scales of vertical advection and diffusion. It also assumes the duration of each egg stage is long relative to the time required for the eggs to achieve a steady-state distribution. To determine whether these conditions apply to the depth profiles of haddock eggs described here (Table 3) requires that the forcing time scales be estimated. In turn, this requires estimates of u, v, W, L_x, L_y, Z, K_x, K_y, K_z, and M.

Wheeler and Miller (1960) measured the terminal velocity of artificially fertilized haddock eggs and reported a value of 8.3×10^{-4}m/s. Bigelow and Welch (1925); Walford (1938); and Wheeler and Miller (1960) measured the specific gravity of artificially fertilized haddock eggs and found early stage eggs had a density of approximately 1023 kg/m^3. Assuming this value applies to the eggs sampled here gives an estimate of $\rho_o - \rho_e$ = 2.3 kg/m^3. Substituting this value into Stokes' and Dallavalles' equations, along with an egg diameter of 1.5×10^{-3} m, yielded a stage I terminal velocity of 1.5×10^{-3} m/s and 1.3×10^{-3} m/

TABLE 5. Regression analyses on the velocity time series. (R^2 is the coefficient of multiple determination; phase is based on an initial time of t_0 = 0813 h (AST) on May 3, 1984 (number of observations = 222 in all cases. Samples span a period of approximately 100 h).

Depth (m)	Mean (cm/s)	Ampl. (cm/s)	Phase (degrees)	R^2
North/South (+/−) component				
16.8	−5.91	39.42	−2.28	0.79
23.2	−5.04	38.78	−3.82	0.82
29.6	−4.39	37.38	−3.28	0.84
36.0	−4.39	35.97	−3.76	0.82
42.4	−4.62	36.45	−4.79	0.85
48.8	−4.86	37.58	−5.21	0.85
55.2	−5.23	39.49	−4.04	0.88
61.6	−4.86	40.48	0.51	0.87
68.0	−4.17	40.75	7.05	0.86
74.4	−3.26	39.45	13.59	0.85
East/West (+/−) component				
16.8	−8.06	49.93	226.63	0.85
23.2	−8.47	48.31	226.27	0.87
29.6	−7.34	47.69	225.93	0.87
36.0	−5.88	47.26	225.71	0.87
42.4	−4.85	48.10	226.38	0.87
48.8	−4.12	49.59	227.34	0.89
55.2	−3.99	49.18	229.83	0.90
61.6	−3.47	47.67	233.20	0.90
68.0	−2.28	44.98	237.24	0.89
74.4	−1.19	42.23	240.15	0.88

s, respectively. An intermediate estimate of W is therefore 1×10^{-3} m/s.

Loder et al. (1988) estimated a coefficient of vertical eddy diffusivity for Browns Bank of 0.02 m²/s which is in the range of typical values for the surface mixed layer (Kullenberg 1976; Csanady 1982; Sundby 1983).

The observed profiles of stage I, II, and III haddock egg concentration suggest an appropriate vertical length scale (Z) is 20 m. A reasonable horizontal length scale ($L_x = L_y$) is 40 km, the diameter of the sampling grid, and the advection rate ($u = v$) is 0.1 m/s. $K_x = K_y$ is assumed to be 50 m²/s, a value appropriate to Browns Bank and the length scale of 40 km (Okubo 1971; Smith 1988).

Using these values the vertical advection (Z/W) and diffusion (Z^2/K_z) time scales are of order 6 and 5 h, respectively. These are small relative to the time scales of mortality (M = 3 d, estimated from data in Table 3), horizontal advection ($L_{x,y}/u,v$ = 5 d) and horizontal diffusion ($L_{x,y}{}^2/K_{x,y}$ = 370 d) and since the vertical adjustment time scale (K_z/W^2 = 3 h) is short relative to the duration of each egg stage we conclude that the egg profiles are in a quasi-steady-state. Thus our theoretical model should provide an explanation for the observed egg profiles.

The exponential decrease in concentration of the stage I, II, and III eggs with increasing depth is consistent with theoretical case (2) where $\rho_e < \rho_o$. The implication that the density gradient has a minor effect on the vertical distribution of these eggs is confirmed by a multiple regression analysis of $\mathrm{Ln}(C(z)+1)$ on z and z^2. The analyses (not shown) indicates the z^2 coefficient, which corresponds to the δ_1 term in equation (11), is not significantly different from zero. The slopes from the regressions of $\ln(C(z)+1)$ against z (Table 4) can therefore be interpreted as estimates of the e-folding scale, δ_2. For stages I, II, and III this scale, as estimated from the median concentrations at each depth (Tables 3 and 4), is 20.4, 23.2, and 33.3 m, respectively.

Using the above estimate of $W = 1 \times 10^{-3}$ m/s and the observed δ_2 value for stage I eggs (20.4 m) indicates K_z during the sampling period is 0.02 m²/s ($K_z = \delta_1 W$), a value which is consistent with previous estimates for Browns Bank (Loder et al. 1988).

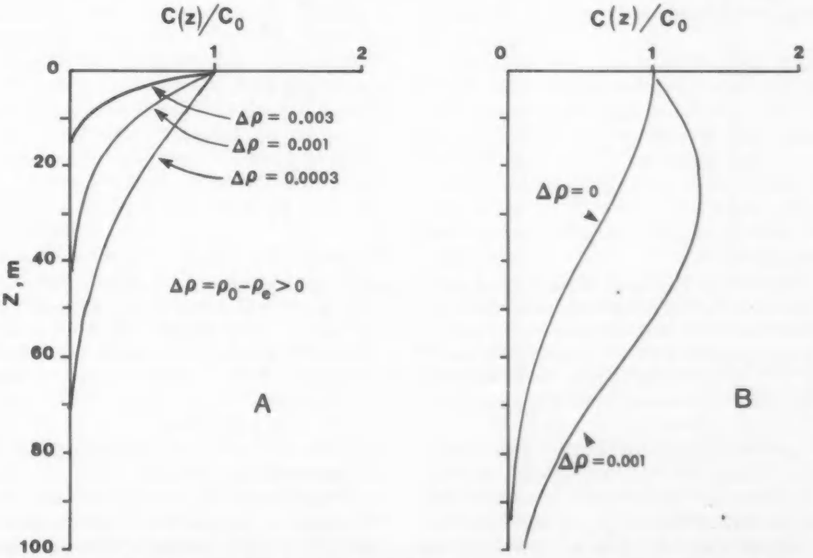

FIG. 3. Model output illustrating the depth distribution of eggs, assuming a range of egg densities, in a linearly stratified water column. (A) $\rho_e < \rho_o$, (B) $\rho_e \geq \rho_o$. The curves were generated by assuming $\rho_w(z) = 1025.3 + 1.17 \times 10^{-4}\ z$, $d = 1.5 \times 10^{-3}$m and K_z = 0.01 m²/s. The values for $\rho_o - \rho_e = \Delta\rho$ were chosen such that $\Delta\rho$ spans the range of typically observed values (see Sundby 1983).

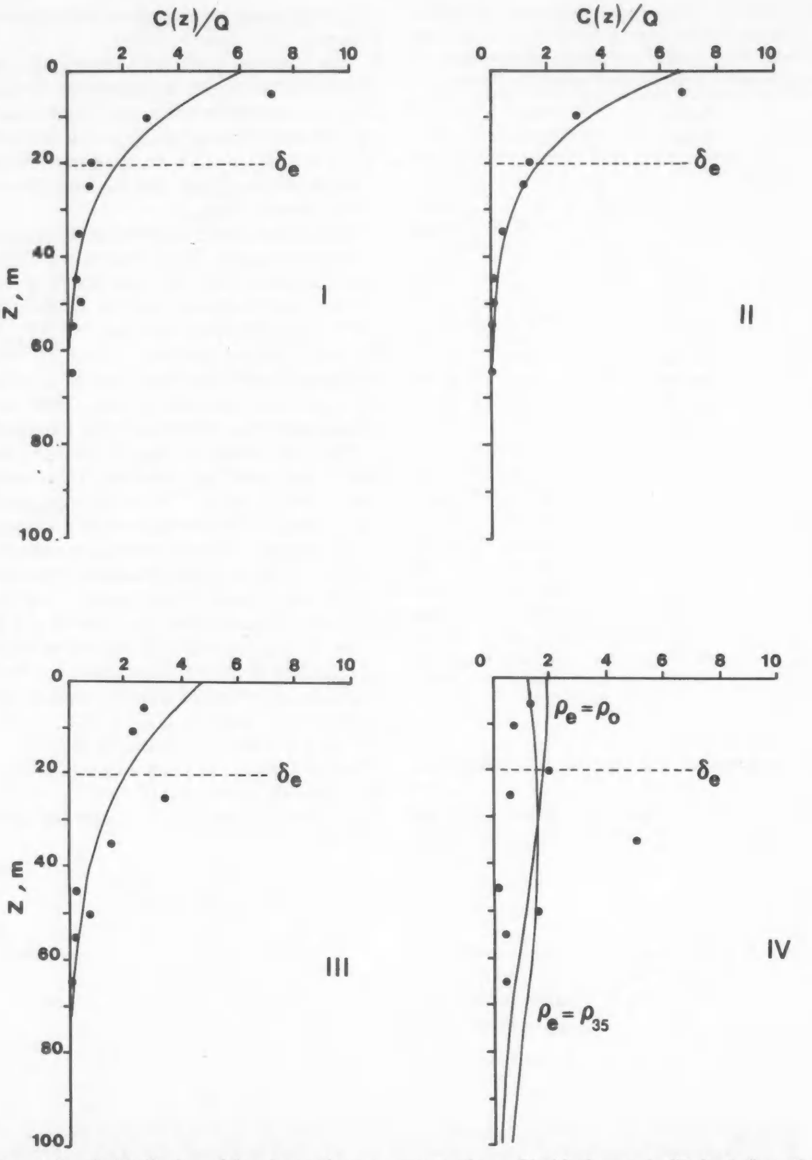

FIG. 4. Depth distribution of the observed mean concentrations of haddock eggs (solid dots). Smooth curves are the profiles generated from the model. I, II, III, and IV refer to egg stages. For stages I to III the smooth curves were generated by using equation (9) and the observed values of δ_2, K_z (0.02 m^2/s), and the density profile. The curves for stage IV were generated by assuming the same K_z and density profile as for the other stages, and by assuming two values of ρ_e chosen to represent $\rho_o - \rho_e = 0$ and $\delta_2 = 35$ m. δ_e is the Ekman depth.

The ratio of the δ_2 values for different stages is indicative of the ratio of the terminal velocities because K_z is the same for all egg stages an assumption consistent with the eggs of all stages occurring in the same water column at the same time. The ratio of stage I to stage III is 0.6 (Table 4) and indicates the stage III terminal velocity is between 0.5×10^{-3} $(0.83 \times 0.6 \times 10^{-3})$ and 0.8×10^{-3}m/s $(1.3 \times 0.6 \times 10^{-3})$. Solving for Dallavalle's terminal velocity resulted in a difference in density between the egg and water of 1.5 kg/m^3. Given a surface water density of 1025.3 kg/m^3, the density of the stage III eggs was 1023.8 kg/m^3.

The estimate of K_z can be further used to compare the depth distribution of the eggs to the depth scale of the surface Ekman layer. The *e*-folding scale of the Ekman layer, assuming a constant K_z and $d\rho_w/dz$, is given by $\delta_e = (2K_z/f)^{1/2}$, where *f* is the Coriolis parameter. The *e*-folding scale of the egg distribution when $\rho_e < \rho_o$ is $\delta_2 = K_z/Wo$. The proportion of the eggs above δ_e is therefore given by

$$\text{(14)} \quad \frac{\int_{-\delta_e}^{0} C(z)\,dz}{\int_{-\infty}^{0} C(z)\,dz} = 1 - e^{-\delta_e/\delta_2}$$

and the proportion below δ_e is given by $\exp(-\delta_e/\delta_2)$. Both of these vary with K_z and W_o whose values depend on the density structure of the water column and the magnitudes of tidal and wind generated velocity shears. In general this dependence may be parameterized such that their influence on the ratios can be investigated.

This is not necessary for the observations described here because we know $K_z = 0.02$ m^2/s and therefore δ_e is approximately -20 m. The δ_e/δ_2 ratios for stage I, II, and III eggs are therefore 1.0, 0.83, and 0.59, respectively. The corresponding proportions of eggs below δ_e are 0.37, 0.44, and 0.55. Consequently, as the eggs develop, a larger proportion of eggs is found below δ_e and a smaller proportion is above δ_e in the high shear zone of the Ekman layer. This relationship is illustrated in Fig. 4 which also shows the depth distribution of stage IV eggs relative to the Ekman depth and model estimates of their distribution. Although the stage IV data are limited, there is a qualitative similarity between their observed and theoretical distributions. This suggests the density of stage IV eggs is similar to, or greater than, the surface water density of $\rho_o = 1025.3$ kg/m^3.

Discussion

The close agreement between the empirical data and theory suggests that we have developed a robust model to explain the vertical distribution of haddock eggs and possibly other planktonic organisms that conform to the model assumptions. The theory developed in this paper represents an extension of Sundby's (1983) homogeneous water column model. Sundby's model predicts an exponential decrease in egg concentration with increasing depth. However, it cannot support a subsurface maximum. Such a maximum is predicted by the theory developed here which is Sundby's model modified to include a depth dependent water density. Although we used a linear gradient in water density and a constant K_z for simplicity, other density and K_z profiles can easily be used. We used a linear density gradient because it was consistent with the density profile of the water column in our sampling area.

The conclusion that the majority of the haddock eggs (all four stages combined) were within the top 50 m of the water column and that the concentration declined exponentially with depth is consistent with previous descriptions of the vertical distribution of haddock eggs (Walford 1938; Colton 1965). This depth pattern is typical of the early egg stages of cod, plaice, and mackerel (Sundby 1983), and pilchard (Coombs et al. 1985), and in the profile of cod/haddock eggs presented by Fridgeirsson (1984). It is inconsistent with the results of Lough (1984) who presented a profile of haddock eggs that increased exponentially with depth. This would suggest that these eggs were negatively buoyant within the sampling depth range.

The conclusion that stage III and perhaps stage IV eggs are distributed more evenly throughout the water column than the earlier stage I and II eggs, conflicts with previous field observations. Walford (1938) and Colton (1965) showed that the vertical distribution of haddock eggs was the same for all developmental stages but Walford (1938) based his conclusions on egg concentrations integrated over broad depth intervals (0–55 m, 55–110 m, and 115–170 m). Our results indicate that the majority of the eggs of all stages are found within the 0–55 m depth interval and it is obvious that Walford's vertical sampling resolution was too coarse to detect ontogenetic changes. The discrepancy with Colton (1965) results from the egg staging systems employed. He used only two stages which corresponded to our stage I and our combined stages II, III, and IV. The concentration of Colton's second stage eggs were probably dominated by stage II (our staging system) and our analysis has shown that their distribution is similar to stage I.

The pattern of ontogenetic variation we describe conflicts with that expected on the basis of previous laboratory measurements (Wheeler and Miller 1960; Moksness and Torstensen 1985). These authors reported that egg density decreased to a minimum during gastrulation (stage II) and then increased toward hatching. Wheeler and Miller (1960) reported that the density of the late stage eggs (stage IV) was intermediate to that of the stage I and II eggs. This suggests that stage II eggs should be more concentrated near the surface than the other stages, and that stage I eggs should be the least concentrated near the surface. Only our stage III and IV eggs are consistent with these expectations. Stage I eggs have a depth profile that is statistically indistinguishable from stage II eggs and more concentrated toward the surface than the stage III and IV eggs.

The vertical distribution of the stage IV haddock eggs we present suggest a subsurface concentration peak which has been subsequently confirmed in follow-up studies reported by Frank et al. (1989) for the same season and region when the survey timing corresponded well with the availability of stage IV eggs. The mean temperature in the upper 35 m during our May 1984 survey was 3.5°C which is 1–2°C lower than the long-term (1946–80) mean sea surface temperature estimated for this region and time by Loucks et al. (1986) and Smith (1989). This could explain the low numbers of stage IV eggs encountered because of a reduced rate of development and a shift in the time of peak spawning.

Peaks have also been shown to exist in the vertical egg profiles of other species such as sprat and pilchard (Coombs et al. 1985) and halibut (Haug et al. 1984, 1986). All of these peaks correspond with density gradients in the water column and could be easily explained by our model.

The potential significance of the vertical distribution of fish eggs to their horizontal transport has long been recognized (see Jacobsen and Johansen 1908). In the case of haddock eggs the existing field evidence indicated ontogenetic variation in the vertical distribution did not occur (discussed previously in this section) and that the majority of the eggs were distributed within the top few tens of metres of the water column (Colton 1965). Colton and Temple (1961) therefore assumed that the horizontal transport of the eggs and larvae was reliably indicated by the trajectories of surface drift bottles, an assumption used to this day for haddock and several other species (e.g. Harding and Trites 1988). This has encouraged the belief that egg and larval transport and dispersal are dominated by the wind, and that inter-annual variation in the wind could explain variation in year-class strength. Significant correlations between indices of the wind variation and year-class strength (Carruthers 1938; Carruthers et al. 1951; Chase 1955) supported this view.

The concept of a highly dispersive egg stage may, however, be misleading. An ontogenetic increase in the specific gravity of the eggs, coupled with vertical mixing, can reduce the wind-induced dispersive influence of Ekman transport. The observations and theory presented here indicate that even under conditions of low wind and weak stratification over 30% of haddock eggs are below the Ekman depth (δ_e). In other words, these eggs are below the depth of wind driven flow. This proportion increases as the eggs develop: more than 50% of the stage III and IV eggs are below δ_e. Under stronger wind conditions, the proportion below will increase because K_z also increases. Surface drift bottles and other indicators of the very near surface wind driven transport would then appear to be poor indicators of haddock egg transport.

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References

AHLSTROM, E. H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60: 107–146.

BIGELOW, H. B., AND W. W. WELCH. 1925. Fishes of the Gulf of Maine. Bull. U.S. Bur. Fish. Vol. 40(1926), part 1, 567 p.

CARRUTHERS, J. N. 1938. Fluctuations in the herrings of the east Anglian autumn fishery, the yield of the Ostend spent herring fishery, and the haddock of the North Sea — in the light of the relevant wind conditions. Rapp. P.-V. Des Reun. Cons. Int. Explor. Mer 107: 10–15.

CARRUTHERS, J. N., A. L. LAWFORD, V. F. C. VELEY, AND B. B. PARRISH. 1951. Variations in brood strength in the North Sea haddock, in the light of relevant wind conditions. Nature (Lond.) 168: 317–319.

CHASE, J. 1955. Winds and temperatures in relation to the brood-strength of Georges Bank haddock. J. Cons. Int. Explor. Mer 21: 17–24.

COLTON, J. B., JR. 1965. The distribution and behavior of pelagic and early demersal stages of haddock in relation to sampling techniques. ICNAF Spec. Publ. 6: 317–333.

COLTON, J. B., JR., AND R. F. TEMPLE. 1961. The enigma of Georges Bank spawning. Limnol. Oceanogr. 6: 280–291.

COOMBS, S. H. 1981. A density gradient column for determining the specific gravity of fish eggs, with particular reference to eggs of the mackerel *Scomber scombrus*. Mar. Biol. 63: 101–106.

COOMBS, S. H., C. A. FOSH, AND M. A. KEEN. 1985. The buoyancy and vertical distribution of eggs of sprat (*Sprattus sprattus*) and pilchard (*Sardina pilchardus*). J. Mar. Biol. Ass. U.K. 65: 461–474.

COOMBS, S. H., D. HARDING, J. H. NICHOLS, AND C. A. FOSH. 1981. The vertical distribution and buoyancy of eggs of plaice (*Pleuronectes platessa* L.) in the southern North Sea. ICES C.M. 1981/G:84.

CSANADY, G. T. 1982. Circulation in the Coastal Ocean. Reidel Publishing Company, 279 p.

DAHLBERG, M. D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessments. Mar. Fish. Rev., March 1979, 1–12.

DORSEY, N. E. 1940. Properties of ordinary water substance. Am. Chem. Soc. Monogr. Ser. No. 81, Reinhold Pub. Corp., New York, NY.

FISH, C. J. 1928. Production and distribution of cod eggs in Massachusetts Bay in 1924 and 1925. Bull. U.S. Bur. Fish. 43(2): 253–296.

FRANK, K. T. 1986. Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 211–222.

FRANK, K. T., F. H. PAGE, AND J. K. MCRUER. 1989. Hydrographic effects on the vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae on the southwestern Scotian Shelf. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

FRIDGEIRSSON, E. 1984. Cod larvae sampling with a large pump off SW-Iceland, p. 317–333. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propogation of Cod *Gadus morhua* L., Flod. Rapp. 1.

GROSSLEIN, M. D., AND R. C. HENNEMUTH. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164: 77–88.

HAUG, T., E. KJORSVIK, AND P. SOLEMDAL. 1984. Vertical distribution of Atlantic halibut (*Hippoglossus hippoglossus*) eggs. Can. J. Fish. Aquat. Sci. 41: 798–804.

1986. Influence of some physical and biological factors on the density and vertical distribution of Atlantic halibut *Hippoglossus hippoglossus* eggs. Mar. Ecol. Prog. Ser. 33: 207–216.

HISLOP, J. R. G., AND M. A. BELL. 1987. Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. J. Fish Biol. 31: 1–20.

HJORT, J. 1914. Fluctuations in the great fisheries of Northern Europe. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 20: 1–13.

1926. Fluctuations in the year classes of important food fishes. J. Cons. Int. Explor. Mer 1: 5–38.

JACOBSEN, J. P., AND A. C. JOHANSEN. 1908. Remarks on the changes in specific gravity of pelagic fish eggs and the transportation of same in Danish waters. Meddelelser Fra Kommissionen for Havundersogelser, Serie: Fiskeri Bind III(2): 1–24.

KOSLOW, T., S. BRAULT, J. DUGAS, AND F. PAGE. 1985. Anatomy of an apparent year-class failure: the early life history of the 1983 Browns Bank haddock (*Melanogrammus aeglefinus*). Trans. Am. Fish. Soc. 114: 478–489.

KULLENBERG, G. 1976. On vertical mixing and the energy transfer from the wind to the water. Tellus, XXVIII(2): 159–165.

LODER, J. W., C. W. ROSS, AND P. C. SMITH. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. 45: 1860–1885.

LOUCKS, R. H., K. R. THOMPSON, AND R. W. TRITES. 1986. Sea surface temperature in the Northwest Atlantic — space and time scales, spectra and spatially smoothed fields. Can. Tech. Rep. Fish. Aquat. Sci. 1430: 80 p.

LOUGH, R. G. 1984. Larval fish trophodynamic studies on Georges Bank: sampling strategy and initial results, p. 395–435. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Selvik [ed.] 1984. The propagation of cod *Gadus morhua* L. Flod. Rapp. 1.

MCKENZIE, R. A. 1940. Nova Scotian autumn cod spawning. J. Fish. Res. Board Can. 5(2): 105–120.

MOKSNESS, E., AND E. TORSTENSEN. 1985. The buoyancy of sprat (*Sprattus sprattus*) eggs and larvae in the Skagerrak area. ICES CM. 1985/L:6, 13 p. (mimeo)

NEEDLER, A. B. 1931. The haddock. Fish. Board Can. Bull. No. XXV., 28 p.

NIHOUL, J. C. J. 1975. Modelling of marine systems. Elsevier, New York, NY.

O'BOYLE, R. N., M. SINCLAIR, R. J. CONOVER, K. H. MANN, AND A. C. KOHLER. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotia Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 183: 27–40.

OKUBO, A. 1971. Oceanic diffusion diagrams. Deep Sea Res. 18: 789–802.

1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, New York, NY. p. 38–40.

PAGE, F. H., AND K. T. FRANK. 1989. Spawning time and egg stage duration in Northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

SAVILLE, A. 1956. Eggs and larvae of haddock (*Gadus aeglinfus* L.) at Faroe. Scottish Home Dept. Mar. Res. 1956, No. 4.

1959. The planktonic stages of the haddock in Scottish waters. Scottish Home Dept. Mar. Res. 1959, No. 3.

SETTE, O. E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: Early life history, including the growth, drift, and mortality of the egg and larval populations. U.S. Fish Wildl. Serv. Fish. Bull. 50: 149–237.

SMITH, P. C. 1988. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

1989. Seasonal and interannual variability off southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

SMITH, W. G., AND W. W. MORSE. 1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. Mar. Ecol. Prog. Ser. 24: 1–13.

SOLEMDAL, P., AND S. SUNDBY. 1981. Vertical distribution of pelagic fish eggs in relation to species, spawning behaviour and wind conditions. ICES C.M. 1981/G:77.

SUNDBY, S. 1983. A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. Deep Sea Res. 30(6a): 645–661.

SUNDNES, G., H. LEIVESTAD, O. IVERSEN. 1985. Buoyancy determination of eggs from the cod (*Gadus morhua* L.). J. Cons. Int. Explor. Mer 29: 249–252.

WALFORD, L. A. 1938. Effects of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank. U.S. Bur. Fish. Bull. 49: 1–73.

WHEELER, C. L., AND D. MILLER. 1960. Aquarium and experimental studies. Ann. Rep. 1960, Mass. Bur. Commer. Fish. Biol. Lab., Woods Hole Circ., 99: 34–37.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, 620 p.

Spawning Time and Egg Stage Duration in Northwest Atlantic Haddock (*Melanogrammus aeglefinus*) Stocks with Emphasis on Georges and Browns Bank[1]

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Literature data was used to examine the hypothesis that variation in the spawning time, defined as the peak in egg abundance, of Northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks is explained by water temperature and to derive calibration curves relating incubation temperature to haddock egg stage duration. Spawning times occurred, on average, in March on Georges Bank, late April/early May on Browns Bank, and in June/July on the Grand Banks. Temperatures at peak spawning overlapped considerably but differed in terms of phase in the annual temperature cycle. Inter-annual variation in spawning time of Georges Bank haddock varied by 3 mo and was significantly correlated with water temperature. Browns Bank haddock spawning varied by only 1 mo and was not correlated with water temperature. Egg stage duration varied with incubation temperature. A power curve best described the relationship and was used to estimate the historical, annual variation in haddock egg stage duration which ranged from 10 to 20 d (mean = 16 d) on Georges Bank and from 10 to 30 d (mean = 18 d) on Browns Bank during 1946–80. Collectively, our analysis calls into question the generality of the assumption of constant spawning times for marine fish species and provides essential information for field measurement of haddock egg production rates, mortality, advection, and dispersal.

On a procédé à une étude bibliographique afin de pouvoir examiner l'hypothèse selon laquelle les variations du moment de la fraie, défini comme étant le maximum d'abondance en oeufs, dépend de la température de l'eau chez les stocks d'aiglefin (*Melanogrammus aeglefinus*) de la partie nord-ouest de l'Atlantique; on voulait aussi dériver des courbes d'étalonnage qui établissaient une relation entre la durée du stade oeuf chez l'aiglefin et la température d'incubation. En moyenne, la fraie avait lieu en mars sur le banc Georges, à la fin avril-début mai sur le banc Browns et en juin-juillet sur les Grands Bancs. Il y avait une considérable superposition des températures observées au maximum de la fraie, mais celles-ci correspondaient à des phases différentes du cycle annuel de température. La variation interannuelle du moment de la fraie de l'aiglefin sur le banc Georges a atteint 3 mo et elle était en corrélation significative avec la température de l'eau. La fraie sur le banc Browns a varié de seulement 1 mo et elle n'était pas en corrélation avec la température de l'eau. La durée du stade oeuf a varié selon la température d'incubation. Une courbe de puissance a le mieux décrit cette relation; elle a été utilisée pour l'estimation de la variation annuelle antérieure de durée du stade oeuf chez l'aiglefin, de 10 à 20 jours (moyenne de 16 d) sur le banc Georges, et de 10 à 30 jours (moyenne de 18 d) sur le banc Browns, entre 1946 et 1980. Dans l'ensemble, notre analyse remet en question le caractère universel de l'hypothèse de moments de fraie constants chez les poissons d'eau salée et en outre, elle apporte des renseignements essentiels à la mesure sur le terrain des taux de production d'oeufs, de mortalité, d'advection et de dispersion chez l'aiglefin.

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Spawning times and locations of marine fishes are generally considered to have evolved so that upon hatching the larval stage emerges into favourable environmental conditions (Scott 1979; Bye 1984). The environmental conditions at the time of emergence may differ from year to year due to variation in the timing and magnitude of the environmental characteristics, variation in the timing of emergence, or to a combination of both. Quantifying the degree of variation and defining the mechanisms causing it is considered to be of prime importance to understanding the dynamics of the early life stages of fish and of year-class size formation. (Rothschild 1986; Cushing 1975).

Analyses of recruitment variation in temperate marine fishes often assume both constant spawning time and egg stage duration. Delays or advances of 10 d or less in spawning time are common and standard deviations of spawning times, estimated from detrended time series, are of order 5 d (Table 1). However, the range in the time of peak spawning may be as large as 30

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TABLE 1. Inter-annual variation in the time of peak spawning for some north temperate and high latitude fish stocks.

Species and stock	Time of observation (yr)	No. of observations	Comments		Source
A) Trends					
Arcto–Norwegian cod	1894–1968	74	Smooth trend in time of peak catch; trend amplitude ca. 10 d		a
	1929–82	54	Linear trend spanning a 1-wk delay in time of median spawning intensity,		b
Southern Bight Plaice	1911–50	8	No detectable trend in		a
Fraser River Sockeye Salmon	1950–66	7	No detectable trend time of peak catch		c
Norwegian Herring	1931–36	6	1–2 wk delay in spawning time		e
B) Variation about trend			Standard deviation (d)	Range	
Newfoundland capelin	1966–82	15	—	19 d	d
Southern Bight plaice	1911–50	8	7	—	a
Norwegian herring	1931–36	6	6	—	a
Georges Bank herring	1963–73	11	5.9	19 d	c
Fraser River sockeye salmon	1950–66	17	4.9	3 wk	a
Arcto–Norwegian cod	1894–1968	74	4.1	20 d	a
	1929–82	54	2.2	35 d	b

[a] Cushing 1969.
[b] Pederson 1984.
[c] Berenbeim and Sigaev 1978.
[d] Leggett et al. 1984.
[e] Rothschild 1986.

d (plus or minus three standard deviations) and since much of the variation in year-class size is often associated with one or two extreme year classes (Shepherd et al. 1984), the assumption of constant spawning times and early life stage durations may not always be appropriate. The importance of taking spawning time into consideration was highlighted for haddock by Chase (1955). The correlation between haddock (*Melanogrammus aeglefinus*) year-class strength on Georges Bank and regional winds was improved considerably when variable spawning times were used to define the temporal window over which the annual estimate of the wind index was calculated.

Haddock generally spawn during the first 6 mo of the year (Hislop 1984; O'Boyle et al. 1984). The duration of the spawning season for each stock is typically 3 to 4 mo with a peak spawning period of about 1 mo. As with other fish species, spawning occurs progressively later in higher latitudes (Bigelow and Welch 1925; Theilacker and Dorsey 1980; Hislop 1984).

The date of spawning in some haddock stocks is highly variable. On Georges Bank, for example, the date of peak spawning can differ by 2 to 3 mo (Marak and Livingstone 1970), a range much greater than for other north temperate marine fish species (Table 1). As with several other species (see Hela and Laevastu 1961 for a review; Colton 1968a; Marak and Livingstone 1970; Smith et al. 1979) spawning date co-varies with water temperature. On Georges Bank anomalously cold (warm) years corresponded with delayed (advanced) spawning such that a 1.5 to 2.0°C change in the mean water temperature during March and April resulted in a 1-mo shift in the time of spawning (Marak and Livingstone 1970). Whether spawning time varies in relation to temperature in other Northwest Atlantic haddock stocks is not known.

Temperature also effects the duration of the egg stage (Walford 1938; Laurence and Rogers 1976) and since sea surface temperatures in the Northwest Atlantic are one of the most variable in the world (Thompson et al. 1988) the duration of the egg stage may also be highly variable. The only documented egg duration — temperature relationship for haddock is linear (Laurence and Rogers 1976), whereas relationships for other species are usually nonlinear (see general review in Blaxter 1969 and recent examples in Table 4). In a recent analysis of several dozen species of marine teleosts, Pauly and Pullin (1988) showed that for a given egg size the relationship between egg stage duration and incubation temperature was curvilinear. Consequently, a nonlinear relationshp may be more appropriate for haddock as well.

The Fisheries Ecology Program was designed to investigate the dynamics of the haddock stock situated in the Southwest Nova Scotia region of the Northwest Atlantic. One objective of this program was to measure rates of egg production, mortality, advection, and dispersal and to compare these with estimates of year-class size. Multiple ichthyoplankton surveys were conducted in each of 3 yr (1983–85) and haddock eggs were routinely sorted into four stages. In order to age the egg stages and to cast the spawning time and egg duration estimates into an historical context an egg duration–temperature calibration relationship was required as well as an examination of historical variation in spawing time.

The objectives of this paper are therefore three-fold. First, review published information on haddock spawning time in the Northwest Atlantic, quantify its variability, relate this to sea surface temperatures and test the hypothesis that spawning time variation in haddock is explained by water temperature. Second, extract from the literature data on temperature and development rate of haddock eggs and derive a robust calibration curve relating incubation temperature to egg stage duration. And third, estimate the historical variation in the duration of the haddock egg stage from time series of sea surface temperatures from southwestern Nova Scotia/Gulf of Maine.

Materials and Methods

Spawning Time

There are at least six haddock stocks in the Northwest Atlantic (Martin 1953; Templeman 1953; Grosslein 1962; Kohler 1968). The location of the major spawning grounds are shown in Fig. 1.

The abundance of early stage eggs from three or more time periods during the expected period of spawning was used to construct annual spawning curves. Only the abundance of early stage eggs were used since the abundance of late stage eggs or larvae may not accurately reflect the true spawning curve (see Hurley and Campana 1989 and Campana et al. 1989). Most of

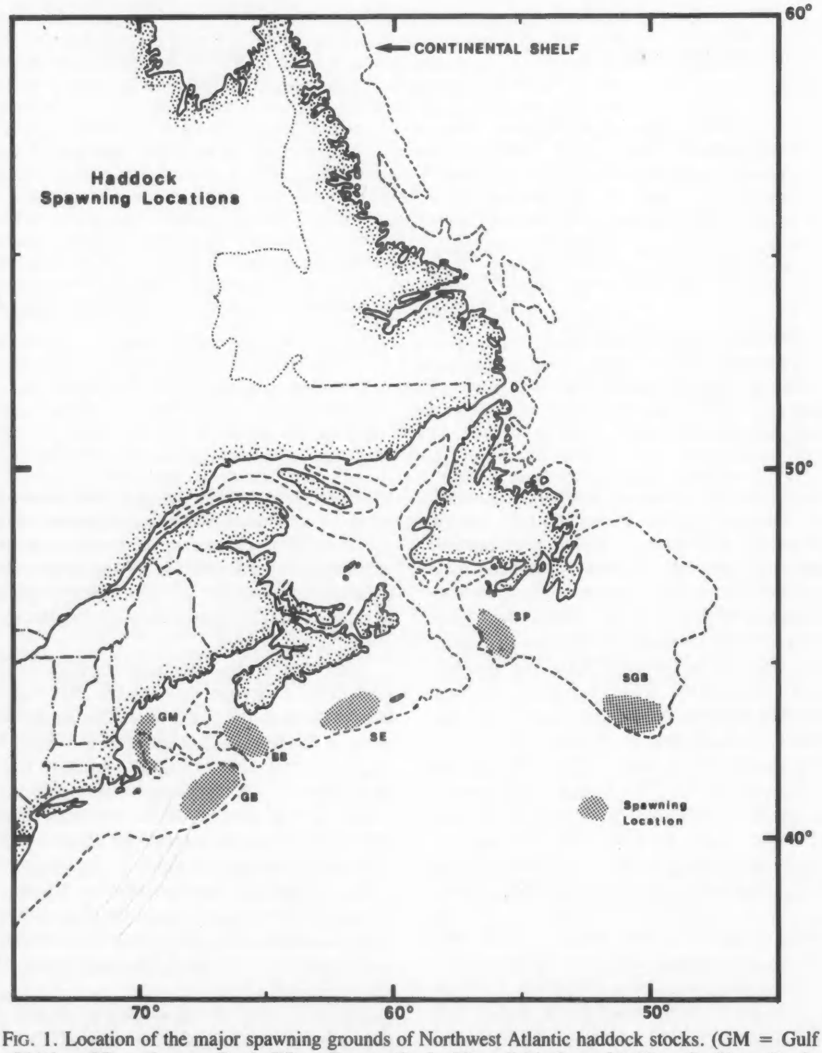

FIG. 1. Location of the major spawning grounds of Northwest Atlantic haddock stocks. (GM = Gulf of Maine; GB = Georges Bank; BB = Browns Bank; SE = Sable-Emerald; SP = St. Pierre Bank; SGB = Southern Grand Bank).

TABLE 2. Spawning times of two haddock populations in the Northwest Atlantic as indicated by ichthyoplankton surveys (P = time of peak egg production; c = reported as a combination of 2 yr, T1 = mean water temperature during March and April at Boothbay Harbour, T2 = mean water temperature during August through March at Boothbay Harbour; — indicates peak spawning extended outside the sampled time period).

Year	Number of cruises					Month								Source	Temperature (°C) T1	T2
Georges Bank		J		F		M		A		M		J	J			
1931	(3)				—	P								a	5.1	7.8
1940	(5)							P		P				b	0.6	5.0
1941	(4)				—	P		P						b	3.6	6.8
1953	(3)				—	P								b	6.8	9.6
1955	(4)		—	P		P								b	5.5	9.4
1956	(5)		—	P		P		P						b	4.2	8.7
1968	(6)							P						d	2.6	6.6
1979–80c							P									
Mean								P								
Browns Bank																
1931	(3)							P						a	5.1	7.8
1953	(3)								P					e	6.8	9.6
1955	(4)								P					f	5.5	9.4
1956	(5)								P					g	4.2	8.7
1979–80c										P	—			d		
1983	(5,8)							P						c,h	3.8	7.9
1984	(5)							P						h	3.2	8.5
1985	(5)								P					h	4.2	8.0
Mean								P								

[a] Walford 1938.
[b] Marak and Livingstone 1970.
[c] Koslow et al. 1985.
[d] Smith and Morse 1985.
[e] Marak and Colton 1961.
[f] Marak et al. 1962a.
[g] Marak et al. 1962b.
[h] Campana et al. 1989.

the spawning time data originated from the Georges and Browns Banks haddock stocks.

On Georges Bank, multiple ichthyoplankton surveys have been conducted annually during the haddock spawning season in at least 16 yr between 1931 and 1983. However, the abundances of early stage eggs were reported in only 8 yr and only in 2 yr was the spawning peak clearly defined (Table 2). In 5 of the 8 yr sampling commenced during peak spawning. Seven of the years (1931–68) were used by Marak and Livingstone (1970) in an analysis of spawning time variation on Georges Bank. The eighth year is reported as 1979–80 since the abundance data was an aggregate of abundances estimated from cruises in the two separate years.

On Browns Bank, there are also 8 yr in which egg abundances were reported for three or more surveys conducted during the winter–spring period. In all years, except the 1979–80 aggregate, the spawning peak was clearly defined (Table 2).

The accuracy of the spawning time estimates is difficult to assess. However, the estimates of egg and larval abundance are typically 2 to 4 wk apart, indicating variation in the spawning time at these or shorter time scales cannot be resolved.

Duration of Haddock Egg Stages

The time and corresponding temperatures for haddock and Atlantic cod (*Gadus morhua*) eggs to develop the morphological characteristics corresponding to the stage descriptions used during the Fisheries Ecology Program (Table 3) was gathered from the literature (Table 4).

Data was extracted from the original sources because many of the sources cited in general reviews of the life history of fish (e.g. Hardy 1978; Bigelow and Welch 1925; Russell 1976; Leim and Scott 1966) are not the original sources and a listing of data derived from these sources showed frequent replication. Although the data were assumed to represent the time required

TABLE 3. Description of the haddock and cod egg stages used in the Fisheries Ecology Program. The designations of Meek (1924) are given for comparison.

Stage	Stage designation of Meek (1924)	Description
I	1–3	From fertilization to the formation of the endoderm, ectoderm and mesoderm; at the end of this stage the blastoderm is starting to overgrow the yolk; includes the morula, blastula, and early gastrula stages.
II	4–6a	From the end of stage I to closure of the blastopore at which time the embryo extends from the animal to vegetal poles (ca. half way around the yolk): during this stage the tail bud, notochord, and optic vesicles appear; the beginning of this stage is marked by the formation of the embryonic shield and embryonic axis.
III	7–9a	From the end of stage II to when the tail can almost touch the head; during this stage the heart begins to beat, the tail bud becomes free of the yolk, and the otoliths begin to develop.
IV	10–12	From the end of stage III to hatching; tail is all the way around yolk sac to the tip of snout and perhaps past; embryo is well pigmented and begins to show characteristic pigment pattern; at the beginning of this stage the upper portion of the eye becomes pigmented.

TABLE 4. List of sources containing the temperature specific stage durations of cod and haddock eggs.

Source	Haddock	Cod
STAGE I		
Meek (1924)		X
Walford (1938)[a]	X	
Bonnet (1939)		X
Marak and Colton (1961)	X	
Fridgeirsson (1978)	X	X
Iversen and Danielssen (1984)[a]		X
STAGE II		
MacIntosh and Prince (1887–88)[b]		X
Meek (1924)		X
Walford (1938)[a]	X	
Bonnett (1939)		X
Marak and Colton (1961)	X	
Nordahl (1970)[b]		X
Schwarz (1971)	X	
Fridgeirsson (1978)	X	X
STAGE III		
MacIntosh and Prince (1887–88)[b]		X
Meek (1924)		X
Bonnet (1939)		X
Marak and Colton (1961)	X	
Fridgeirsson (1978)	X	X
STAGE IV		
Earll (1878)		X
Baird (1884)[b]		X
Cunningham (1885)[b]	X	
McIntosh and Prince (1887–88)[b]		X
Rognerud (1889)[b]		X
Dannevig (1895)[c]	X	X
Brice (1898)	X	X
Apstein (1909)[d]		X
Meek (1924)		X
Fish (1928)		X
Walford (1938)	X	
Bonnet (1939)		X
Woodworth et al. (1946)		X
Oppenheimer (1955)		X
Marak and Colton (1961)	X	
Svetovidov (1962)[b]	X	
Westerhagen 1968)	X	
Solemdal (1970)		X
Schwarz (1971)	X	
Laurence and Rogers (1976)	X	X
Fridgeirsson (1978)	X	X
Skreslet and Danes (1978)		X
Iversen and Danielssen (1984)		X

[a] Read from a graph.

[b] Original source cited. Data taken from Hardy (1978).

[c] Original source cited. Data taken from Jacobsen and Johansen (1908); Allen (1917); and Laurence and Rogers (1976).

[d] Original source cited. Data taken from Postolaky (1968).

to develop to the end of each egg stage, the end of a stage does not occur instantaneously. The transition period is, however, assumed to occur on a time scale of hours, a period that is brief relative to the stage duration.

Several expressions are commonly used to describe the relation between incubation temperature (*T*) and egg stage duration (*A*; see review in Blaxter 1969) and we examined the data in relation to the four most common forms: power, exponential, linear, and second-order polynomial curves (Table 5). The power and exponential curves were fit by logarithmic transformation to their linear forms; because some of the incubation temperatures were less than or equal to 0°C temperature data were first transformed by adding the value of 2. The second-order polynomial was fit by using the deviation $(T-\bar{T})$ of each temperature (*T*) from the mean $(\bar{T})$ to avoid potential computational difficulties arising from a significant correlation between the linear (*T*) and quadratic (T^2) terms (Neter et al. 1983). The significance of the power and exponential curve regressions was determined by testing $Ho{:}\ b=0$ using a *t*-test (Zar 1974). For the polynomial regressions the null hypotheses were $Ho{:}\ b=c=0$ (*F*-test; Zar 1974) and $Ho{:}\ c=0$ and $Ho{:}\ b=0$ (*t*-test; Zar 1974). Comparisons between pairs of regression slopes and elevations were made using *t*-tests (Zar 1974). All regressions were performed using the MINITAB statistical package (Ryan et al. 1981) which employs standard least squares procedures.

Temperature

The temperature time series from Boothbay Harbour, Maine, available as monthly means measured at a depth of 5.5 m, was used to evaluate the relationship between spawning time and water temperature. The Boothbay Harbour temperatures represent the longest continuous time series of water temperatures available for this region (1906–present) and in spite of being a coastal series, it is indicative of low frequency trends in temperature from the offshore surface and subsurface waters of the

TABLE 5. Functional form of age–temperature relationships for fish eggs.

Relationship	Species	Source(s)
Polynomial (first-order): $A = a + bT$		
Haddock	(*Melanogrammus aegelfinus*)	Laurence and Rogers (1976)
Cod	(*Gadus morhua*)	Laurence and Rogers (1976)
Polynomial (second-order): $A = a + bT + cT^2$		
Garfish	(*Belone belone*)	Fonds et al. (1974)
Exponential: $A = a \exp(bT)$		
Pacific sardine	(*Sardinops sagax*)	Smith (1973)
Cod	(*Gadus morhua*)	Hela and Laevastu (1961) Thompson and Riley (1981)
Herring	(*Clupea harengus*)	Hela and Laevastu (1961)
Pacific sardine	(*Sardinops melanosticta*)	Hela and Laevastu (1961)
Power: $A = aT^b$		
Sole	(*Solea solea*)	Riley (1974)
Pacific sardine	(*Sardinops caerulea*)	Lasker (1964)
Capelin	(*Mallotus villosus*)	Frank and Leggett (1981)
Sprat	(*Sprattus sprattus*	Thompson et al. (1981)
Hake	(*Merluccius merluccius*)	Coombs and Mitchell (1982)
Other nonlinear forms		
Plaice	(*Pleuronectes platessa*)	Ryland et al. (1975)

TABLE 6. Product–moment correlation coefficients relating monthly mean BoothBay Harbour water temperature (Drinkwater and Trites 1987) to the monthly median sea surface temperatures (SST) on Georges and Browns Banks (1946–80). SST's are those used by Thompson et al. (1988). (ns = not significant at the 0.05 level).

Month	Georges Bank	Browns' Bank
Jan.	0.59	0.49
Feb.	0.56	0.46
Mar.	0.59	0.18 ns
Apr.	0.53	0.31 ns
May	0.47	0.64
Jun.	0.38	0.44
Jul.	0.57	0.40
Aug.	0.62	0.60
Sept.	0.58	0.59
Oct.	0.52	0.50
Nov.	0.30 ns	0.29 ns
Dec.	0.77	0.47

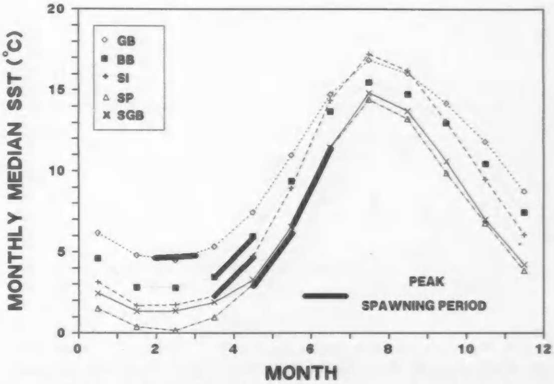

FIG. 2. Estimated mean date of peak haddock spawning in relation to spawning ground location and the annual cycle in sea surface temperature (SST). The duration of each peak spawning period was assumed to be 1 mo. Spawning dates for Georges Bank (GB) and Browns Bank (BB) are taken from Table 2. Egg abundance data collected in 1979 (O'Boyle et al. 1984) was used to estimate spawning date in the Sable-Emerald (SE) stock. Spawning times in the Southern Grand Bank (SGB) and St. Pierre Bank (SP) stocks were taken from Templeman et al. (1978); Templeman and Bishop (1979); and Fitzpatrick and Miller (1979) who estimated spawning time from several years of ichthyoplankton and adult catch and maturity data.

Scotian Shelf and Gulf of Maine (Lauzier 1965; Colton 1968b) and weakly indicative of the higher frequency monthly mean offshore sea surface temperatures (Table 6). Unfortunately, continuous temperature time series for the offshore spawning areas that encompass the range of years for which spawning time is available, 1931 to 1985 (see Results), are not available.

The Boothbay data were averaged over March and April, April and May, and August through March. The March and April or April and May averages corresponded with the expected time of peak spawning on Georges and Browns Banks, respectively, and may be indicative of an environmental cue acting to trigger spawning near the end of gonad maturation. A similar index was used by Colton (1968a) and Marak and Livingstone (1970) to examine the relationship between spawning time on Georges Bank and water temperature. The August through March average was used since (i) it corresponds with the period of gonadal development in haddock from the Gulf of Maine and Scotian Shelf region (Homans and Vladykov 1954; Overholtz 1987; Waiwood and Buzeta 1989) and (ii) it removes some of the high frequency variation that is not coherent over large spatial scales (Akenhead et al. 1981).

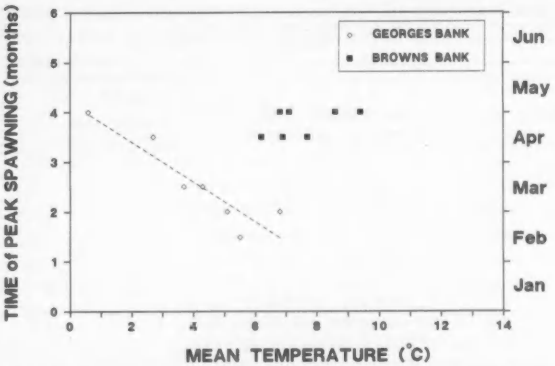

FIG. 3. Relationship between the date of peak haddock spawning on Browns and Georges Bank and the average sea surface temperature (SST). Mean SST was calculated as the average of the monthly mean SST in March and April for Georges Bank spawning and April and May for Browns Bank spawning. The dashed line is the least squares regression line ($Y = 4.2 - 0.4X$; $r^2=0.85$, $p<0.02$), relating the date of peak spawning on Georges Bank (Y) to mean temperature (X). The date of peak spawning is represented as Jan = 0.5, Feb = 1.5, Mar = 2.5, etc.

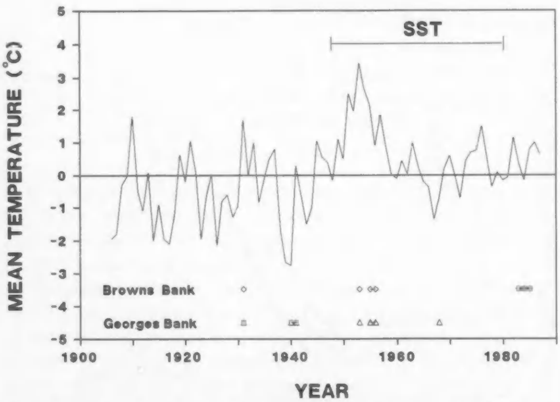

FIG. 4. Time series of the annual anomalies in the average of the March and April monthly mean sea surface temperatures (SST) at Boothbay Harbour. Anomalies were calculated as deviations from the average temperature [(March + April)/2] calculated over the full length of the Boothbay time series (1906–87). Also shown is the period (1946–80) of the SST's derived by Thompson et al. (1988) and the years in which estimates of the date of peak spawning are available for the Browns (open diamonds) and Georges (open triangles) Bank haddock stocks.

The monthly median sea surface temperatures (SST, 1946–80) estimated by Thompson et al. (1988) for the major spawning regions on the continental shelves off the eastern coast of North America were used to examine the historical variation in the stage duration of haddock eggs.

Results

Spawning Time

The mean time of peak spawning for the Northwest Atlantic haddock stocks superimposed on the annual cycle in the long-term (1946–80) average monthly median sea surface temperatures (Loucks et al. 1986) clearly shows a delay in spawning time as one proceeds northward from Georges Bank to the Grand Banks (Fig. 2). This delay is approximately 1 mo between Georges and Browns Bank, and approximately 2 to 3 mo between Georges Bank and the Grand Banks. Peak spawning on Georges Bank usually occurs in mid- to late March, on Browns Bank in late April or early May, on Sable-Emerald banks in late April and early May, and on the Southern Grank Bank and St. Pierre Bank in June or July.

Peak spawning occurred in all regions when the mean sea surface temperature fell between 2 and 10°C. Although the phasing of the annual temperature cycle was similar for the five regions, the annual mean temperature decreased from Georges to the Southern Grand Banks. Temperatures within the 2 to 10°C range occur at progressively later dates with increasing latitude such that spawning on Georges Bank coincided with the onset of spring warming and in the other areas spawning occurred after it (Fig. 2).

On Georges Bank the time of peak egg production varied by 3 mo from early or mid-February to late April or early May (Table 2). This represents a deviation from the mean of about +/− 45 d. On Browns Bank the date of peak spawning ranged from mid-April to early May, a range of less than 1 mo (Table 2).

The relationship between spawning time and the average Boothbay Harbour water temperatures during March and April, April and May, and August through March was evaluated in order to test the hypothesis that variation in spawning time is explained by water temperature. Spawning date on Georges Bank was significantly and negatively correlated with all three temperature indices (March–April: $r^2=0.85$, $p<0.005$, Fig. 3; April–May: $r^2=0.78$, $p<0.01$; August–March: $r^2=0.78$, $p<0.01$) whereas no significant correlations were found between spawning date on Browns Bank and the three temperature indices (March–April: $r^2=0.27$, $p>0.20$; April–May: $r^2=0.25$, $p>0.20$, Fig. 3; August–March: $r^2=0.40$, $p>0.10$). The relationship for Browns Bank may, however, be biased since spawning time data was available only in relatively warm years. The spawning time data for Georges Bank encompassed both relatively warm and cold years (Figs. 3 and 4).

Egg Duration as a Function of Incubation Temperature

The age of each egg stage and the corresponding incubation temperatures derived from the literature are shown in Figs. 5a–d. The number of observations and the temperature range (ca. −1 to 16°C) was greatest for stage IV eggs. At temperatures below 2°C there were 11 determinations (four investigations) of the age of stage IV cod eggs and only one determination of the age of haddock eggs. Stages I through III contain fewer observations spread over a narrower temperature range (2 to 16°C). Only two observations exist for stage III haddock.

It could be criticized that by combining data from age determinations made on eggs of differing origin (different females, different stocks, and different years) and cultured under different experimental conditions, variation in age at a given temperature would increase. The data for stage IV cod eggs indicates that this does not, however, obscure the relationship (Fig. 6). With the exception of three values, the ages deviated only slightly from the mean (+/− 2 d). Pooling of the data within species therefore appears reasonable and even advanta-

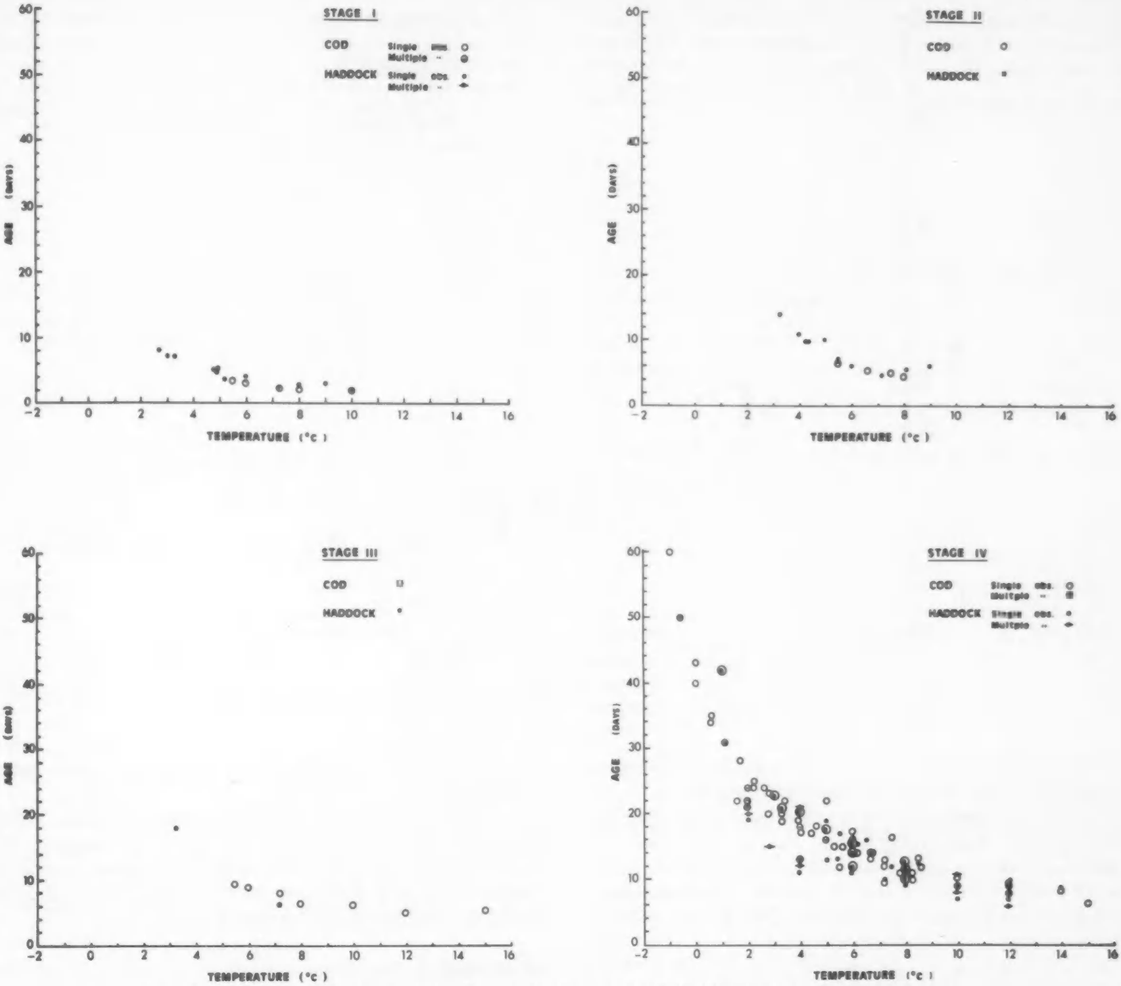

FIG. 5. Scattergrams of age versus temperature for four stages (I, II, III, IV) of cod and haddock eggs.

geous given that it allows estimation of a mean age–temperature relationship for a range of stocks and temperatures.

The relationship between temperature and egg age was generally nonlinear and the three nonlinear relationships (power, exponential, and second-order polynomial) yielded statistically significant results. Although second-order polynomials explained more of the stage I to III variance than the power curves, they explain a relatively low proportion of the variance in the stage IV eggs. Since it is common practice to use the same functional form for each stage (for example: Thompson and Riley 1981; Coombs and Mitchell 1982), the functional form explaining the greatest amount of variance in the stage IV eggs was retained. This choice also avoids the tendency for the polynomial equations to predict ages that are inconsistent with the general trend of the data, when temperatures outside the range of observation are used. The exponential relationship usually accounted for a smaller proportion of the variance than either the power or polynomial relationships. The power curve explained the greatest proportion of the variance in stage IV egg duration and the second largest proportion of the variance in the other three stages (Table 7). Analyses of the stage IV residuals showed they were normally distributed with no obvious trends about the fitted curve.

A statistical comparison between the power curves for cod and haddock within each egg stage was considered inappropriate due to possible biases associated with differences in the range of temperatures used to incubate the eggs of each species. The power curves were therefore re-fit using the data falling within a common temperature range and the slopes were then compared (Table 8). The slopes of the stage IV relationships were not significantly different. The elevation of the cod relationship exceeded that of haddock by 4 d. This is similar to the 2 to 3 d difference found by Laurence and Rogers (1976). Dannevig (1895; cited in Laurence and Rogers 1976) found that the hatching times of cod and haddock were almost identical. The slopes of the stage I and II haddock regressions were no longer significant due to the narrow, common temperature range.

Although the time to hatching differed between the two species the relationships derived from the combined cod and haddock data may be more useful because the early stages of cod and haddock eggs cannot be visually distinguished from each other. In addition, the absolute differences between the ages at

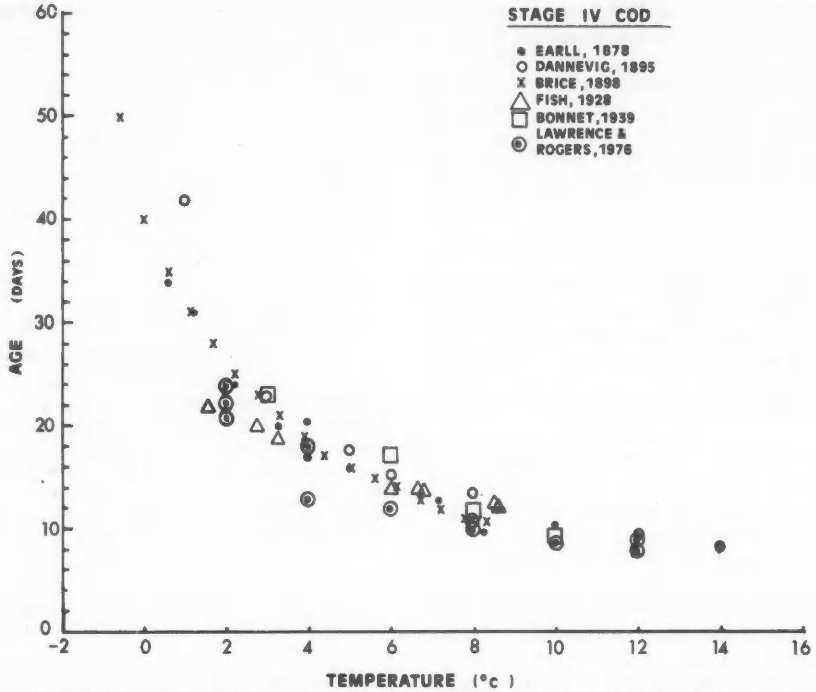

FIG. 6. Scattergram of age versus temperature for stage IV cod eggs as a function of experiment.

hatching for cod and haddock were relatively small and the sample size would increase for stages I, II, and III.

Power curve regressions of the pooled data were highly significant for all stages (Table 9; Fig. 7). The fitted curves for stages II and III cross over at temperatures below 3°C. A similar feature was evident in the temperature dependent egg development curves reported for hake by Coombs and Mitchell (1982).

Historical Variation in Egg Duration

Historical variation in the age of haddock eggs at the time of hatching was determined for the month of peak spawning, the month prior to peak spawning and the month after peak spawning for each year during the period 1946–80. Ages were calculated using the combined cod/haddock power curve relationship (Table 9) and the monthly median sea surface temperatures for Georges Bank and Browns Bank (Fig. 8a,b). In the analysis the months of peak spawning were assumed constant and equal to the long-term mean of April on Browns Bank and on Georges Bank peak spawning was calculated from the relationship between Boothbay Harbour temperatures and spawning time (Fig. 3).

The egg duration on Georges Bank varied by a factor of two, ranging from 10 to 20 d over the 34-yr period (Fig. 9a). During peak spawning the mean egg stage duration was 15.5 d. On Browns Bank the egg stage duration was more variable, ranging from 10 to 30 d (Fig. 9). The mean duration during peak spawning was 18.6 d and similar to that on Georges Bank. The greater variability on Browns Bank can be explained by the lower temperatures typical of this region during March, April, and May in comparison to Georges Bank (Fig. 8) and the amplification of these low temperatures by the age–temperature power curve relationship.

Trends in the age time series differed between banks. Visual inspection of the age series for Georges Bank suggests the occurrence of a low frequency trend with a pseudo-period of approximately 25 yr and an amplitude of about 5 d. On Browns Bank this trend was not as prominent.

Discussion

It is generally believed that the time of spawning in marine teleosts has evolved so that the period when the early life stages are present coincides with an environmental regime that is suitable for their survival and development (Cushing 1975; Scott 1979; Bye 1984) and perhaps with a circulation regime that enables the spatial continuity of the larvae to be maintained (Iles and Sinclair 1982). With respect to survival and development Cushing (1967, 1969, 1975) has suggested that in north temperate regions the date of teleost spawning is constant and occurs prior to the spring bloom so that larvae can emerge during the bloom. Variation in the timing of the spring bloom may therefore cause recruitment variation. This mechanism has been suggested as an explanation for increase in the abundance of cod and haddock stocks in the North Sea during the 1960's (the 'gadoid outburst'; Cushing 1984).

Haddock throughout the North Atlantic spawn during the spring to summer period (Hislop 1984; Bergstad et al. 1987; Fig. 2) with spawning time being progressively latter in more northerly and cooler latitudes (Fig. 2). Whether spawning in each stock occurs during the same phase of the annual production or biomass cycles remains uncertain. In the North Sea spawning occurs during late March to early May (Hislop 1984)

TABLE 7. Power curve ($A = a(T+2)^b$) regression analyses of egg stage duration (A in days) on temperature (°C) using the full data set. Designation: P = probability level; Rej. = reject null hypothesis; Acc. = cannot reject null hypothesis; R^2 = coefficient of determination unadjusted for the degrees of freedom; n = sample size).

	Haddock	Cod
Stage I		
Log(a)	1.82	1.51
b	−1.38	−1.14
R^2	89.8	87.6
n	11	6
Ho: $b=0$	Rej. ($P<0.001$)	Rej. ($P<0.01$)
Ho: slopes equal	Acc. ($P>0.2$)	
Ho: elevations equal	Rej. ($P<0.001$)	
Stage II		
Log(a)	2.09	1.80
b	−1.38	−1.15
R^2	76.3	96.5
n	11	6
Ho: $b=0$	Rej. ($P<0.001$)	Rej. ($P<0.001$)
Ho: slopes equal	Acc. ($P>0.2$)	
Ho: elevations equal	Rej. ($P<0.005$)	
Stage III		
Log(a)	—	1.63
b	—	−0.77
R^2	—	89.6
n	2	7
Ho: $b=0$	—	Rej. ($P<0.005$)
Stage IV		
Log(a)	1.89	1.87
b	−0.89	−0.82
R^2	73.3	93.0
n	60	100
Ho: $b=0$	Rej. ($P<0.001$)	Rej. ($P<0.001$)
Ho: slopes equal	Acc. ($P>0.2$)	
Ho: eelvations equal	Rej. ($P<0.001$)	

TABLE 8. Power curve ($A = a(T+2)^b$) regression analyses of egg stage duration (A in days) on temperature (°C) using only those observations within the temperature range common to both the haddock and cod data set. Designations: same as in Table 7)

	Haddock	Cod
Stage I		
Log(a)	1.23	1.51
b	−0.78	−1.14
R^2	40.8	87.6
n	5	6
Ho: $b=0$	Acc. ($P>0.20$)	Rej. ($P<0.01$)
Common temperature range	5–11	
Stage II		
Log(a)	1.65	2.06
b	−0.95	−1.42
R^2	40.6	86.0
n	5	5
Ho: $b=0$	Acc. ($P>0.20$)	Rej. ($P<0.050$)
Common temperature range	5.2–8.5	
Stage IV		
Log(a)	1.89	1.91
b	−0.89	−0.86
R^2	73.3	89.0
n	60	92
Ho: $b=0$	Rej. ($P<0.001$)	Rej. ($P<0.001$)
Common temperature range	1–14	
Ho: slopes equal	Acc. ($P>0.5$)	
Ho: elevations equal	Rej. ($P<0.001$)	

TABLE 9. Summary of regression analyses on the combined data set (cod and haddock) assuming a power curve ($D = a(T+2)^b$) relationship between egg stage duration (D in days) and temperature (T in °C).

	Log(a)	b	R^2	n	*Ho:* $b=0$
Regression					
STAGE I	1.90	−1.50	90.3	17	Rej. ($P<0.001$)
STAGE II	2.12	−1.43	85.8	17	Rej. ($P<0.001$)
STAGE III	1.90	−1.03	87.6	9	Rej. ($P<0.001$)
STAGE IV	1.88	−0.85	86.6	158	Rej. ($P<0.001$)
Constant slope					
STAGE I	1.32	−0.85	—	17	—
STAGE II	1.58	−0.85	—	17	—
STAGE III	1.73	−0.85	—	9	—
STAGE IV	1.88	−0.85	86.6	158	Rej. ($P<0.001$)

and, in general, coincides closely with the spring maximum in *Calanus finmarchicus* (Cushing 1984). On Georges Bank peak egg and larval abundances may occur earlier than the spring maximum in zooplankton biomass. Spawning, particularly during the 1970's and 1980's, occurred in March or early April (Fig. 2) and the maximum abundance of haddock larvae (1977–80) occurred in April (Sherman et al. 1984) in accordance with the 10 to 20 d duration of the egg stage. The spring maximum in zooplankton biomass occurred in May or June (Sherman et al. 1984; Davis 1987). The 1 to 2 mo delay between peak haddock egg and/or larval abundance and peak zooplankton biomass therefore suggests that eggs released later in the spawning season hatch into a water column with higher zooplankton biomass. On Emerald Bank both haddock spawning and the spring maximum in zooplankton production peak in April and May (Fig. 2; McLaren et al. 1989). However, the production peak may not be indicative of the biomass peak (Davis 1987).

The spawning time of Georges Bank haddock is highly variable contrary to the general assumption of a constant spawning time among marine teleosts (Fig. 3). Colton (1968a) and Marak and Livingstone (1970) showed that interannual variation in spawning time of the Georges Bank stock was as large as 3 mo (Table 2) and that spawning time was qualitatively related to temperature. The relationship we derived was based on data presented by both Marak and Livingstone (1970) and Walford (1938) and although this encompasses the years from 1931 to 1968, the relationship holds true for more recent years. For example, maturity data collected during 1977 to 1983, indicates the spawning period ranged between the last 2 wk of March and the third week of April, with spawning usually occurring in late March or early April (Overholtz 1987). In 1979–80 egg abundance estimates indicated peak spawning occurred in late March (Table 2; Smith and Morse 1985). The predicted time of spawning, based on the mean sea surface temperatures at Boothbay Harbour during March and April of 1977 to 1983 (mean temperature ranged from 2.4 to 3°C), is also mid-March to early April.

On Browns Bank interannual variation in spawning time appears to be much smaller than on Georges Bank (Fig. 3), and

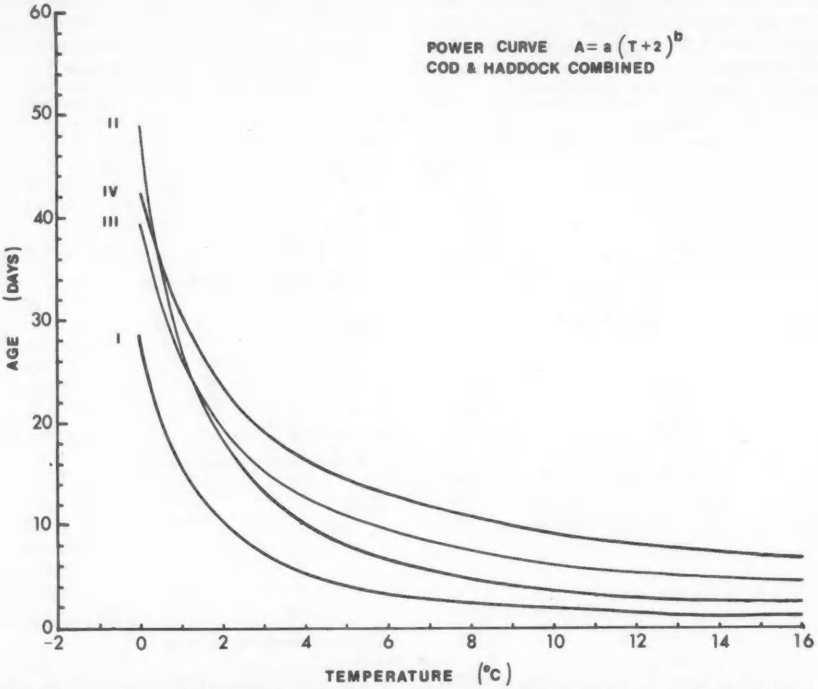

FIG. 7. Power curves relating egg stage duration to incubation temperature. Curves are those estimated from the pooled cod and haddock data set. The parameters for each curve are given in Table 9.

is within the range typically reported for other north temperate marine species (Table 1). The estimated mean date of peak spawning is late April (Table 2; Fig. 3). This period is consistent with the April to June period estimated by Waiwood and Buzeta (1989) from maturity data collected between 1970 and 1986 and with the April or earlier date inferred from egg abundance data collected in 1979 (only two surveys; O'Boyle et al. 1984). The Boothbay Harbour temperatures during these years were similar to those used in the Browns Bank spawning time–temperature relationship.

Despite the limitations of the data it is interesting to speculate on why spawning time is dependent on temperature on Georges Bank but not so on Browns Bank. Adult haddock are not strong migrators and the general distribution may (Barents Sea: Begstad et al. 1987) or may not change with trends in the water temperature (Georges Bank–Gulf of Maine, Colton 1972). Most haddock are caught in areas where the water temperature falls within a temperature range that is narrow relative to what is available (Bergstad et al. 1987; Overholtz 1987; Waiwood and Buzeta 1989). It might be expected, therefore, that haddock avoid much of the temperature variation and that a spawning time–temperature dependency would not exist. On the other hand the magnitude of temperature anomalies are usually only a few degrees and, with the possible exception of stocks near the southern or northern limits of the species distribution, are often within the haddock's preferred temperature range of approximately 3 to 10°C (Bergstad et al. 1987; Waiwood and Buzeta 1989). The Georges Bank stock is near the southern limit of the distributional range of this species in the western Atlantic and as such its reaction to environmental change may be greater relative to the Browns Bank haddock, which is closer to the middle of the distributional range. The lack of a relationship between spawning time and temperature on Browns Bank may therefore be a reflection of our inability to detect a response that is less pronounced than on Georges Bank. In addition the Boothbay Harbour temperature series is only weakly correlated with the sea surface temperatures in the Browns Bank region (Table 6) and the available spawning time data encompasses only a limited temperature range (Fig. 4).

It is therefore not unreasonable to suggest that the time of spawning in other haddock stocks of the western North Atlantic has also varied in response to the climatic trend in water temperature. This has potentially important consequences for both management and research strategies. The fishery for the Browns Bank haddock stock is regulated, in part, by the use of a spawning time closure policy (Halliday 1988). If such a policy is to be effective for this, or for other stocks, the closure period must either be quite broad, including the February through May period for the Georges Bank stock, or it must be very flexible so that closure periods can be assigned on a year to year basis with the period in each year being defined by taking water temperature into consideration. From a research perspective attempts to isolate the causal mechanisms of recruitment fluctuation should take in to consideration the timing of spawning on a year to year basis. Making the assumption that spawning time is constant may lead to faulty interpretations of the data.

With respect to the dependence of haddock egg duration on incubation temperature the power curve relationship derived here is consistent with that used for several other species (Blaxter 1969; Pauly and Pullin 1988; Table 4) and is preferrable to the linear relation used by Laurence and Rogers (1976). Due to the paucity of observations on haddock development rates at

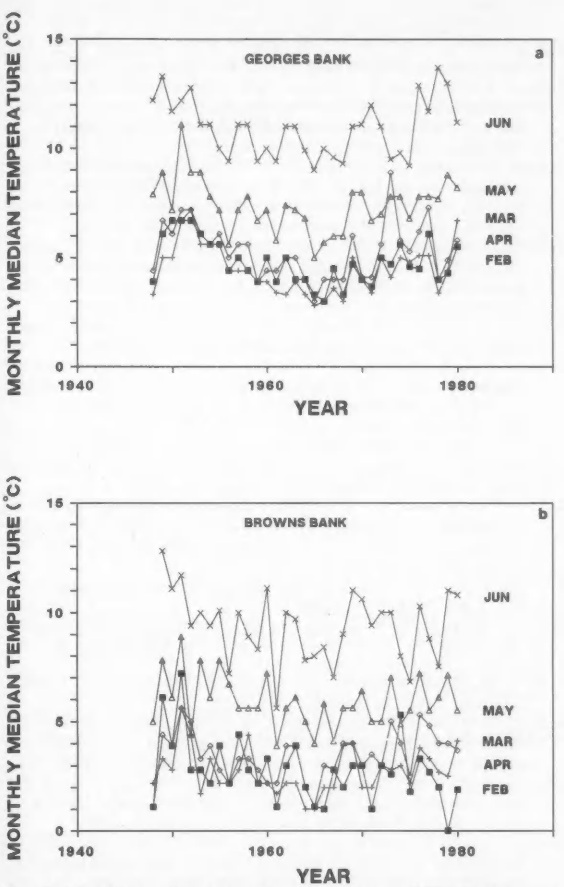

FIG. 8. Monthly median sea surface temperatures (SST) for February through June for the period 1948–80; (a) Georges Bank and (b) Browns Bank.

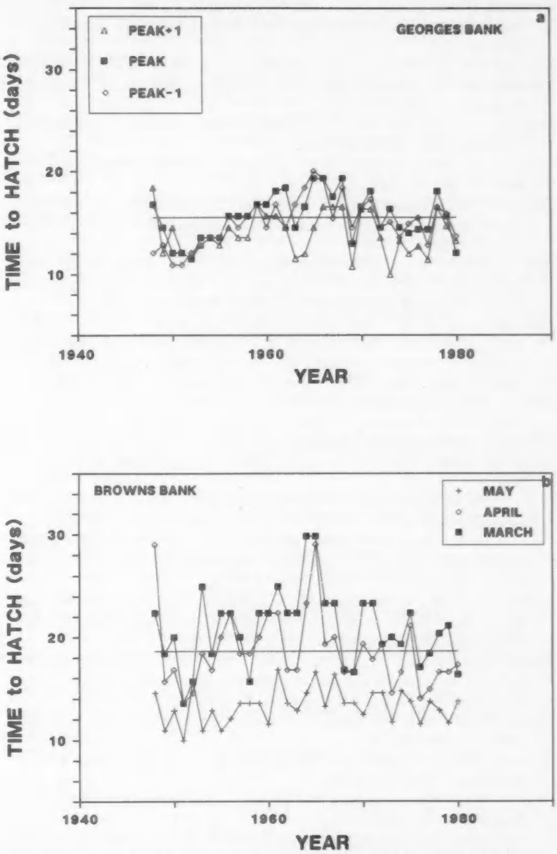

FIG. 9. Age of haddock eggs at the time of hatching on (a) Georges Bank and (b) Browns Bank for the period 1948–80. The month of peak spawning on Georges Bank was estimated from Boothbay Harbour sea surface temperatures using the regression equation in Fig. 3. Peak spawning on Browns Bank was assumed to occur in April.

temperatures below 2°C and the generally few observations for stages I through III, the power curves were defined by combining the available information on haddock and cod. These relationships compare well with the times to hatch given by Thompson and Riley (1981) for cod and are probably adequate for both cod and haddock. The temperatures during the haddock spawning season seldom fall below 2°C, although in some years such a situation may exist (Loucks et al. 1986; Thompson et al. 1988).

The temperature–time to hatch relationship reconstructed from the time series of sea surface temperatures (1948–80) revealed that the egg duration ranged from 10 to 20 d on Georges Bank and 8 to 30 d on Browns Bank. Unlike spawning time the variance in the duration of the egg stage, appears to be greater on Browns than on Georges Bank. This may be due to the later spawning time of the Browns Bank haddock, since the rate of increase in vernal warming is greatest during the Browns Bank spawning. In the context of a simple exponential mortality model with a constant mortality coefficient of 10% per day, this range represents an order of magnitude difference in absolute mortality during the egg stage. This suggests that egg mortalities in different stages of the annual spawning curve and in different stocks may be quite different. Consequently, mortality trajectories of cohorts spawned at different times in the spawning cycle may be quite different.

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References

AKENHEAD, S. A., B. D. PETRIE, C. K. ROSS, AND D. M. WARE. 1981. Ocean climate and the marine fisheries of Atlantic Canada. An appraisal. Bedford Institute of Oceanography, Rep. Ser./BI-R-81-8/June 1981, 121 p.

ALLEN, E. J. 1917. The age of fishes and the rates at which they grow. J. Mar. Biol. Assoc. U.K. 9: 399–424.

BERENBEIM, D. Y., AND I. K. SIGAEV. 1978. On the correlation between water temperature and the spawning times for Georges Bank herring. ICNAF Selected Papers, No 3, p. 57–59.

Bergstad, O. A., T. Jorgensen, and O. Dragesund. 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fish. Res. 5(1987): 119–161.

Blaxter, J. H. S. 1969. Development: eggs and larvae, p. 177–252. *In* W. S. Hoar and D. J. Randall [ed.] "Fish Physiology: Volume III," Academic Press, New York, NY.

Bigelow, H. G., and W. W. Welch. 1925. Fishes of the Gulf of Maine. Bull. U.S. Bur. Fish. (1924) 40: 1–567.

Bonnet, D. D. 1939. Mortality of the cod egg in relation to temperature. Biol. Bull. 76 (3): 428–441.

Brice, J. J. 1898. A manual of fish-culture, based on the methods of the United States Commission of Fish and Fisheries. Appendix to U.S. Comm. Fish. Rep. 23 (1897): 1–340.

Bye, V. J. 1984. The role of environmental factors in the timing of reproductive cycles, p. 187–205. *In* G. W. Potts and R. J. Wootton [ed.] "Fish reproduction: strategies and tactics," Academic Press, New York, NY.

Campana, S. E., K. T. Frank, P. C. F. Hurley, P. A. Koeller, F. H. Page, and P. C. Smith. 1989. Survival and abundance of young cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): (This issue).

Chase, J. 1955. Winds and temperatures in relation to the brood-strength of Georges Bank haddock. J. Cons. Perm. Int. Explor. Mer 21: 17–24.

Colton, Jr., J. B. 1968a. A comparison of current and long-term temperatures of continential shelf waters, Nova Scotia to Long Island. ICNAF Res. Bull. 5: 110–129.

1968b. Recent trends in subsurface temperatures in the Gulf of Maine and contiguous waters. J. Fish. Res. Board Can. 25(11): 2427–2437.

1972. Temperature trends and the distribution of groundfish in continental shelf waters, Nova Scotia to Long Island. Fish. Bull. 70(3): 637–657.

Colton, Jr., J. B., W. B. Smith, A. W. Kendall, Jr., P. L. Berrien, and M. P. Fahay. 1979. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. Fish. Bull. 76: 911–915.

Coombs, S. H., and C. E. Mitchell. 1982. The development rate of eggs and larvae of the hake, *Merluccius merlucius* (L.) and their distribution to the west of the British Isles. J. Cons. Int. Explor. Mer 40: 119–126.

Cushing, D. H. 1967. The grouping of herring populations. J. Mar. Biol. Ass. U.K. 47: 193–208.

1969. The regularity of the spawning season of some fishes. J. Cons. Int. Explor. Mer 33: 81–92.

1975. Marine ecology and fisheries. Cambridge University Press, New York, NY. 278 p.

1984. The gadoid outburst in the North Sea. J. Cons. Int. Explor. Mer 41: 159–166.

Davis, C. S. 1987. Components of the zooplankton production cycle in the temperate ocean. J. Mar. Res. 45: 947–983.

Earll, R. E. 1878. A report on the history and present condition of the shore cod fisheries of Cape Ann, Mass., together with notes on the natural history and artificial propagation of the species. U.S. Comm. Fish. Rep. 6 (1878): 685–740.

Fish, C. J. 1928. Production and distribution of cod eggs in Massachusetts Bay in 1924 and 1925. Bull. U.S. Bur. Fish. 4: 253–296.

Fitzpatrick, C., and R. J. Miller. 1979. Review of spawning time and locations for some commercial finfish on the Newfoundland and Labrador coasts. Fish. Mar. Serv. Tech. Rep. 905: v + 14p.

Fonds, M., H. Rosenthal, and D. F. Alderdice. 1974. Influence of temperature and salinity on embryonic development, larval growth and number of vertebrae of the garfish, *Belone belone*, p. 509–525. *In* J. H. S. Blaxter [ed.] "The early life history of fish," Springer-Verlag.

Frank, K. T., and W. C. Leggett. 1981. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic, and biological factors. Can. J. Fish. Aquat. Sci. 38: 1327–1338.

Fridgeirsson, E. 1978. Embryonic development of five species of gadoid fishes in Icelandic waters. Rit Fiskideildar (Reykjavik) Vol. V, No. 6.

Grosslein, M. D. 1962. Haddock stocks in the ICNAF convention area. ICNAF Redbook 1962, Part III, p. 124–131.

Halliday, R. G. 1988. Use of seasonal spawning area closures in the management of haddock fisheries in the Northwest Atlantic. NAFO Sci. Studies 12: 27–36.

Hardy, Jr., J. D. 1978. Development of fishes of the mid-atlantic bight. An atlas of egg, larval and juvenile stages. Volume II. Anguillidae through Syngnathidae. U.S. Dept. Interior, Fish Wildl. Ser., FWS/OBS-78/12, 458 p.

Hela, I., and T. Laevastu. 1961. Fisheries hydrography. Fishing News (Books) Ltd., 137 p.

Hislop, J. R. G. 1984. A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North Sea, p. 311–329 *In* G. W. Potts and R. J. Wootton [ed.] "Fish reproduction: strategies and tactics," Academic Press, New York, NY.

Homans, R. E. S., and V. D. Vladykov. 1954. Relation between feeding and the sexual cycle of the haddock. J. Fish. Res. Board Can. 11: 535–542.

Hurley, P. C. F., and S. E. Campana. 1989. The distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in the waters off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): (This issue).

Iversen, S. A., and D. S. Danielssen. 1984. Development and mortality of cod (*Gadus morhua* L.) eggs and larvae in different temperatures, p. 49–65. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L., Flod. Rapp. 1.

Jacobsen, J. P., and A. C. Johansen. 1908. Remarks on the changes in specific gravity of pelagic fish eggs and the transportation of same in Danish waters. Meddelelser Fra Kommissionen For Havundersogelser, Serie: Fiskeri, Bind III, Nr. 2, p. 1–24.

Kohler, A. C. 1968. Fish stocks of the Nova Scotia Banks and Gulf of St. Lawrence. Fish. Res. Board Can. Tech. Rep. 80: 9 p, 16 Fig.

Koslow, J. A., S. Brault, J. Dugas, and F. H. Page. 1985. Anatomy of an apparent year-class failure: early life history of the 1983 Browns Bank haddock *Melanogrammus aeglefinus*. Trans. Am. Fish. Soc. 114: 478–489.

Lasker, R. 1964. An experimental study of the effect of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia 1964: 399–405.

Laurence, G. C., and C. A. Rogers. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) J. Cons. Int. Explor. Mer 36 (3): 220–228.

Lauzier, L. M. 1965. Long-term temperature variations in the Scotian shelf area. ICNAF Spec. Publ. 6: 807–816.

Leggett, W. C., K. T. Frank, and J. E. Carscadden. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 41: 1193–1201.

Leim, A. H., and W. B. Scott. 1966. Fishes of the Atlantic Coast of Canada. Fish. Res. Board Can. Bull. No. 155. 465 p.

Loucks, R. H., K. R. Thompson, and R. W. Trites. 1986. Sea surface temperatures in the northwest Atlantic — space and time scales, spectra and spatially smoothes fields. Can. Tech. Rep. Fish. Aquat. Sci. 1430: 80 p.

Marak, R. R., and J. B. Colton, Jr. 1961. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank–Gulf of Maine area, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep., Fish. No. 398.

Marak, R. R., J. B. Colton, Jr., and D. B. Foster. 1962a. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank–Gulf of Maine area, 1955. U.S. Fish Wildl. Serv., Spec. Sci. Rep., Fish. No. 411.

Marak, R. R., J. B. Colton, Jr., D. B. Foster, and D. Miller. 1962b. Distribution of fish eggs and larvae, temperature, and salinity in the Georges Bank–Gulf of Maine area, 1956. U.S. Fish Wildl. Serv., Spec. Sci. Rep., Fish. No. 412.

Marak, R. R., and R. Livingstone, Jr. 1970. Spawning dates of Georges Bank haddock. ICNAF Res. Bull., No. 7, p. 56–58.

Martin, W. R. 1953. Identification of major groundfish stocks in subarea 4 of the Northwest Atlantic Convention area. ICNAF Ann. Proc., Vol 3, p. 57–61.

McLaren, I. A., M. J. Tremblay, C. J. Corkett, and J. C. Roff. 1989. Copepod production on the Scotian Shelf based on life-history analyses and laboratory rearings. Can. J. Fish. Aquat. Sci. 46: 560–583.

Meek, A. 1924. The development of the cod (*Gadus callarias*, L.). Ministry of Agriculture and Fisheries. Fishery Investigations. Series II. Vol. VII. No. 1. 26 p.

Neter, J., W. Wasserman, and M. H. Kutner. 1983. Applied linear regression models. Richard D. Irwin, Inc., 547 p.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 183: 27–40.

Oppenheimer, C. H. 1955. The effect of marine bacteria on the development and hatching of pelagic fish eggs, and the control of such bacteria by antibiotics. Copeia 1955: 43–49.

Overholtz, W. J. 1987. Factors relating to the reproductive biology of Georges Bank haddock (*Melanogrammus aeglefinus*) in 1977–83. J. Northwest Atl. Fish. Sci. 7: 145–154.

Pauly, D., and R. S. V. Pullin. 1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fish. 22(4): 261–271.

Pedersen, T. 1984. Variation of peak spawning of Arcto-Norwegian cod (*Gadus morhua* L.) during the time period 1929–1982 based on indices estimated from fishery statistics. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] "The propagation of cod *Gadus morhua* L.," Flod. Rapp. 1, 1984: 301–316.

Postolaky, A. I. 1968. The life cycle pattern of Labrador cod, *Gadus morhua* L. in ICNAF subarea 2. ICNAF Spec. Publ. 7, p. 139–144.

Riley, J. D. 1974. The distribution and mortality of sole eggs (*Solea solea* L.) in inshore areas, p. 39–52. *In* J. H. S. Blaxter [ed.] "The early life history of fish," Springer-Verlag.

Rothschild, B. J. 1986. Dynamics of marine fish populations. Harvard University Press, 277 p.

Russell, F. S. 1976. The eggs and planktonic stages of British marine fishes. Academic Press, New York, NY. p. 4–19.

Ryan, T. A., B. L. Joiner, and B. F. Ryan. 1981. Minitab reference manual. Minitab Project, Statistics Department, Pennsylvania State Univ., Pa.

Ryland, J. S., J. H. Nichols, and J. P. Sykes. 1975. Effect of temperature on the embryonic development of the plaice, *Pleuronectes platessa* L. (Teleostei). J. Exp. Mar. Biol. Ecol. 18: 121–137.

Schwarz, A. 1971. Swimbladder development and function in the haddock, *Melanogrammus aeglefinus* L., Biol. Bull. 141: 176–188.

Scott, D. B. C. 1979. Environmental timing and the control of reproduction in teleost fish. Symp. Zool. Soc. Lond. 44: 105–132.

Shepherd, J. G., J. P. Pope, and R. D. Cousens. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. R.-V. Reun. Cons. Int. Explor. Mer 185: 255–267.

Sherman, K., W. Smith, W. Morse, M. Berman, J. Green, and L. Ejsymont. 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18: 1–19.

Skreslet, S., and G. J. Danes. 1978. Seaward transport of eggs of coastal cod (*Gadus morhua*) from spawning grounds in Ullsfjord North Norway. Astarte 11: 11–20.

Smith, P. E. 1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer. 164: 282–291.

Smith, W. G., and W. W. Morse. 1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. Mar. Ecol. Prog. Ser. 24: 1–13.

Solemdal, P. 1970. Intraspecific variations in size, buoyancy and growth of eggs and early larvae of Arcto–Norwegian cod, *Gadus morhua* L., due to parental and environmental effects. ICES CM 1970/F:28, 8 p., 8 Fig.

Templeman, W. 1953. Knowledge of divisions of stocks of cod, haddock, redfish and American plaice in subareas 3 and 2 of the Northwest Atlantic Convention area. ICNAF Ann. Proc. Vol. 3, p. 62–66.

Templeman, W., and C. A. Bishop. 1979. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, at St. Pierre Bank. ICNAF Res. Bull. No. 14, p. 77–83.

Templeman, W., V. M. Hodder, and R. Wells. 1978. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the Southern Grand Bank. ICNAF Res. Bull. No. 13, p. 53–65.

Theilacker, G., and K. Dorsey. 1980. Larval fish diversity, a summary of laboratory and field research. Intergovernmental Oceanographic Commission, Workshop Rep. No. 28, "Workshop on the effects of environmental variation on the survival of larval pelagic fishes," p. 105–142.

Thompson, K. R., R. H. Loucks, and R. W. Trites. 1988. Sea surface temperature variability in the shelf-slope region of the Northwest Atlantic. Atmos.–Ocean, 26(2): 282–299.

Thompson, B. M., S. P. Milligan, and J. H. Nichols. 1981. The development rates of sprat (*Sprattus sprattus*) eggs over a range of temperatures. ICES CM 1981/H:15 (mimeo).

Thompson, B. M., and J. D. Riley. 1981. Egg and larval development studies in the North Sea cod (*Gadus morhua* L.). Rapp. R.-V. Reun. Cons. Int. Explor. Mer 178: 553–559.

Waiwood, K. G., and M.-I. Buzeta. 1989. The reproductive biology of Southwest Scotian Shelf haddock (*Melanogrammus aeglefinus*). Can. J. Fish. Aquat. Sci. 46: 0000–0000.

Walford, L. A. 1938. Effects of currents and distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank. Bull. U.S. Bur. Fish. 49: 1–73.

Westernhagen, H. von. 1968. Versuche zur Erbrutung der Eier des Schellfishes (*Melanogrammus aeglefinus* L.) unter Kombinierten Salzgehalts — und Temperature bedingungen. Ber dt. wiss. Kommn Meeresforsch. 19: 270–287.

Woodworth, K., H. G. Kewalramani, M. P. Motwani, and J. H. Orton. 1946. Artificial fertilization of cod (*Gadus callarias* Linn.) at Port Erin. Nature (Lond.) 157: 700.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., 620 p.

Hydrographic Effects on the Vertical Distribution of Haddock (*Melanogrammus aeglefinus*) Eggs and Larvae on the Southwestern Scotian Shelf[1]

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Relationships between the density (sigma-*t*) structure of the water column and the depth distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae in May of 1985 and 1986 were investigated. During the early embryonic period the egg concentration decreased exponentially with depth; this contrasted sharply with stage IV eggs which showed a subsurface maximum, the location of which was determined by their specific gravity. Depth of the centre-of-mass (Z_{cm}) of stage IV eggs ranged from 13 to 47 m over the survey area whereas the sigma-*t* associated with the Z_{cm} depth varied only slightly (CV = 0.4%) about a mean of 25.58. In stratified offshore waters, haddock eggs were aggregated at middepth but exhibited a progressively more uniform vertical distribution towards the weakly stratified nearshore. Where low-density water (sigma-*t* < 25.5) occurred nearshore, eggs were concentrated at the deepest sampling stratum, suggesting that peak egg concentrations were below this level or possibly on the bottom. The depth distribution of haddock larvae was identical to that of late-stage eggs and was therefore established by buoyancy changes occurring during the embryonic period. Day and night Z_{cm} was similar, averaging 28 and 31 m, respectively, and stability of the depth distribution of larvae appears to persist well into the juvenile period.

Les rapports entre la structure de densité (sigma-*t*) de la colonne d'eau et la répartition selon la profondeur des oeufs et des larves d'aiglefin (*Melanogrammus aeglefinus*) ont été étudiés en mai 1985 et 1986. Au début de la période embryonnaire, la concentration d'oeufs diminuait exponientiellement en fonction de la profondeur; ce phénomène contraste grandement avec la situation des oeufs de stade IV qui semblent atteindre un maximum sous la surface, maximum dont l'emplacement a été déterminé par la gravité spécifique des oeufs. La profondeur du centre de la masse (Z_{cm}) des oeufs de stade IV variait de 13 à 47 m dans la zone étudiée, tandis que sigma-*t* associé à la profondeur Z_{cm} ne variait que légèrement (CV = 0.4 %) autour d'une moyenne de 25.58. Dans les eaux du large stratifiées, les oeufs d'aiglefin formaient des agrégats à mi-profondeur, mais présentaient une distribution verticale progressivement plus uniforme en s'approchant des eaux faiblement stratifiées plus près du rivage. Lorsque les eaux de l'avant-plage présentaient une faible densité (sigma-*t* <25.5), les oeufs étaient concentrés dans la couche d'échantillonnage la plus profonde, ce qui laisse croire que les concentrations d'oeufs maximales se situaient sous ce niveau ou possiblement sur le fond. La répartition en profondeur des larves d'aiglefin était identique à celle des oeufs de stade terminal et a par conséquent été établie à partir des changements de flottabilité survenant pendant la période embryonnaire. Le Z_{cm} diurne et nocturne était semblable, atteignant en moyenne 28 et 31 m, respectivement et la stabilité de la répartition en profondeur des larves semble persister bien avant dans la période juvénile.

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There are at least seven recognized stocks of haddock (*Melanogrammus aeglefinus*) in the Northwest Atlantic (Scott and Scott 1988). According to Needler (1929), haddock are most abundant in water of salinities >32‰, and the low salinities characteristic of the nearshore and the Gulf of St. Lawrence are responsible for their scarcity in these regions. The spawning grounds of haddock are generally located on offshore banks of the Continental Shelf where both aggregations of haddock in spawning condition and high concentrations of eggs and larvae have been observed (Grosslein and Hennemuth 1973; Colton et al. 1979; Fitzpatrick and Miller 1979; Scott 1983; O'Boyle et al. 1984). Haddock eggs and larvae appear to be retained on the banks for varying amounts of time, and larval behaviour as well as circulation features associated with the banks are believed to underlie their temporal persistence in these offshore regions (Sinclair and Iles 1988). The general question of causes of population richness among marine fishes has been addressed by Sinclair (1988) who argued that larval behaviour is paramount to the formation and maintenance of discrete stocks.

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Egg and larval retention on offshore banks has been shown or inferred for those stocks of haddock spawning on the southern Grand Bank (Templeman and Hodder 1965), Scotian Shelf (O'Boyle et al. 1984), and Georges Bank (Bolz and Lough 1984; Lough 1984; Sherman et al. 1984). The simplest hypothesis to explain retention is that advection and diffusion are sufficiently low so as not to displace the offspring very far from the spawning site. However, the hypothesis given the greatest emphasis to explain retention is vertical migration, both diurnal and ontogenetic, during the larval and postlarval period (Sinclair and Iles 1988). This hypothesis should be deferred until simpler hypothesis are evaluated and developmental events during the embryonic period are fully explored.

The tendency for a species to form local populations may, in part, be connected with the specific gravity of the eggs. The specific gravity of marine fish eggs is largely determined by the ambient salinity of waters where maturing fish occur, through its effect on the osmolarity of the ovarian fluid (Solemdal 1967, 1971, 1973; Craik and Harvey 1987). After fertilization the influence of external salinity on the buoyancy of developing, pelagic eggs is slight and, in most cases, insignificant (Kanoh 1955; Solemdal 1971, 1973; Hempel 1979; Coombs et al. 1985; Riis-Vestergaard 1983; Craik and Harvey 1987). These recent results are consistent with the earlier viewpoint held by Walford (1938) that pelagic fish eggs tend to remain in water of the same specific gravity as that in which they were fertilized. Alternatively, pelagic eggs may experience greater mortality in anomalous water masses. Spawning site selection and the associated hydrographic conditions may, therefore, be very important in defining the distributional range of the eggs and larvae.

Different physiological races of a single fish species can have genetically based differences in egg density which adapt them to regional conditions. Plaice (*Pleuronectes platessa*) spawning in the brackish waters of the Baltic Sea produce eggs of lower specific gravity than their marine counterparts, and this adaptation ensures that their eggs will remain buoyant in the immediate spawning environment (Solemdal 1973). Fall-spawning populations of pilchard (*Sardina pilchardus*) in the western English Channel produce eggs that are more buoyant than those of summer spawners, possibly in response to increased mixing associated with the higher autumnal winds (Coombs et al. 1985). Egg buoyancy differences also exist between species. Such is the case for two gadoids (Norway pout (*Trisopterus esmarkii*) and Atlantic cod (*Gadus morhua*)) spawning in the Norwegian Coastal Current (Mork et al. 1983) and sprat (*Sprattus sprattus*) and pilchard spawning in the waters around Plymouth (Coombs et al. 1985). Analysis of the buoyancy characteristics of haddock eggs could provide an explanation for their persistent occurrence in the vicinity of offshore banks and their absence in nearshore waters.

Our objectives in this paper are to examine the spatial variation in the vertical distribution of haddock eggs in relation to the density (sigma-*t*) structure of the water column over a grid of stations ranging from the southwestern Scotian Shelf to the approaches to the Bay of Fundy. Particular emphasis is paid to the depth variation in the terminal stage of egg development in haddock because this depth range of hatching is important to early larval survival. In the analysis we assume that late-stage haddock eggs are distributed in relation to their neutral buoyancy, as suggested by Page et al. (1989) and as shown for Atlantic halibut (*Hippoglossus hippoglossus*) (Haug et al. 1986). We expected that haddock eggs would become denser towards hatching as do the eggs of mackerel (*Scomber scombrus*) (Ware and Lambert 1985), cod (Sundnes et al. 1965), and walleye pollock (*Theragra chalcogramma*) (Nishiyama et al. 1984) and that the vertical distribution of haddock larvae and late-stage eggs would be similar. If true, this might explain how haddock larvae become associated with certain depth strata, such as the thermocline as noted by Miller et al. (1963) on Georges Bank. Finally, analysis of the depth distribution of larvae is presented to provide a preliminary assessment of the pattern of vertical migration characteristic for the early feeding stages of haddock.

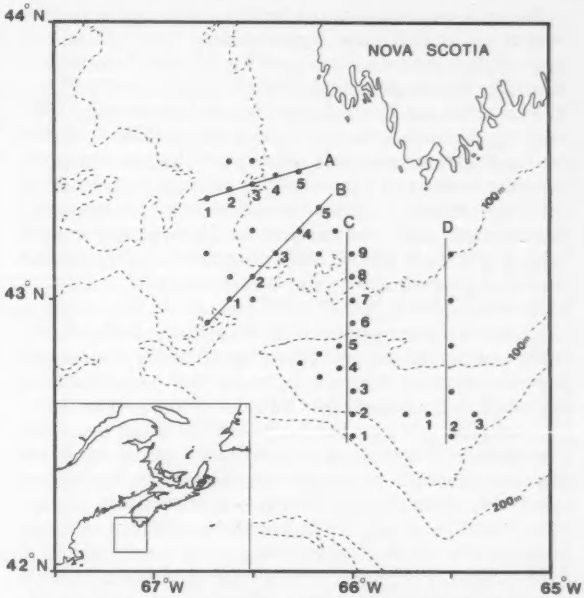

FIG. 1. Coastal and shelf region off southwestern Nova Scotia. Station positions are shown for the 1985 and 1986 May cruises. Individual cruise coverage is shown in Fig. 2. Most stations are distributed along four (A – D) cross-shelf transects. Depth contours are in metres.

Materials and Methods

The vertical distribution of haddock eggs and larvae was studied on the southwestern Scotian Shelf/eastern Gulf of Maine region during 8–23 May 1985 (28 stations) and 9–20 May 1986 (34 stations). Sampling stations were located along four cross-shelf transects (Fig. 1). The southernmost stations were located over Browns Bank, an important spawning ground for haddock during April–May (O'Boyle et al. 1984), and the northerly stations included the nearshore waters off Nova Scotia. The stations were broadly distributed to ensure that egg and larval collections would be made in very different hydrographic regimes. The inshore areas and western cap of Browns Bank are known to be vertically well mixed (Smith 1983, 1989) whereas the remaining areas exhibit a range of stratification intensity (Fournier et al. 1984).

The vertical distribution of haddock eggs and larvae was determined from discrete depth sampling conducted in both years using a small-scale version of the BIONESS (Sameoto et al. 1980). The sampling depths were 5, 10, 20, 35, 45, 55, and 65 m in 1985 and 5, 10, 20, 30, 35, 45, and 55 m in 1986. Each depth was sampled for 7–8 min, the opening of each of the seven 333-μm-mesh nets was 0.25 m^2, and towing speeds generally averaged 1.5 m/s. A CTD positioned on top of the net frame provided real-time measurements of temperature, salinity, depth, pitch, roll and flow rate. Water density was calculated from each pair of temperature and salinity measurements using the one atmosphere International Equation of State of Seawater, 1980 (UNESCO 1981).

All samples were preserved in 4% formalin buffered with sodium borate. All fish eggs and larvae were identified, sorted, and counted under a binocular dissection microscope. Haddock eggs can only be distinguished from cod during the later stages of development (Markle and Frost 1985), although the timing of our surveys was too late to encounter cod eggs in significant quantities. This was subsequently verified by the low proportion (<5%) of late-stage cod eggs collected in May of each year. Therefore, all eggs were counted as haddock and were separated into four developmental stages (after Markle and Frost 1985): stage I, fertilization to the formation of a visible embryonic axis, includes the morula, blastula, and early gastrula stages; stage II, midgastrula to approximate time of blastopore closure, embryo is wrapped half way around the yolk; stage III, end of stage II to the time tail reaches or could reach the snout; stage IV, prehatching, characteristic pigmentation pattern evident. Dead eggs were not included in the analysis and were only infrequently encountered. Total length measurements were made of all haddock larvae using an ocular micrometer. Haddock eggs and larvae were expressed as number per 100 m^3 of water filtered.

Variation in the vertical distribution of each haddock egg stage and 1-mm size categories of haddock larvae from 3 to 9 mm was evaluated by calculating the depth of the centre of mass of the distribution, Z_{cm} (metres):

$$Z_{cm} = \sum_{i=1}^{7} (p_i Z_i) = \sum_{i=1}^{7} (C_i Z_i) / \sum_{i=1}^{7} C_i$$

where p_i and C_i are, respectively, the proportion and concentration (number per 100 m^3) of eggs or larvae in the ith depth interval and Z_i is the depth of the ith stratum. An additional aspect of the vertical distribution was evaluated for haddock eggs, i.e. the vertical dispersion. The index used as a measure of the vertical dispersion was

$$s = 1/7 \sum_{i=1}^{7} (p_i - \bar{p})^2$$

where $\bar{p}$ is the average percentage of eggs per stratum. The value of s is minimum when the eggs are evenly distributed over the water column ($s = 0$ when $p_i = \bar{p}$) and maximum when all the eggs are concentrated in one stratum ($s = 6 \cdot \bar{p}^2$).

Results

Horizontal Distribution

During the May 1985 survey, haddock eggs were found throughout the grid. The highest concentrations (>10/100 m^3) were observed south of 43°10′N (Fig. 2) at stations over Browns Bank, the principal haddock spawning ground, and along the 100-m isobath. Over the entire survey area the average egg density was 10/100 m^3 (range 0.4–30/100 m^3), with 70% of the stations sampled yielding egg concentrations in excess of 5/100 m^3 (Fig. 2). The May 1986 survey revealed a similar distribution of haddock eggs as in 1985, but contrasted sharply with 1985 in terms of abundance. Egg densities greater than 5/100 m^3 occurred at less than 25% of the stations sampled.

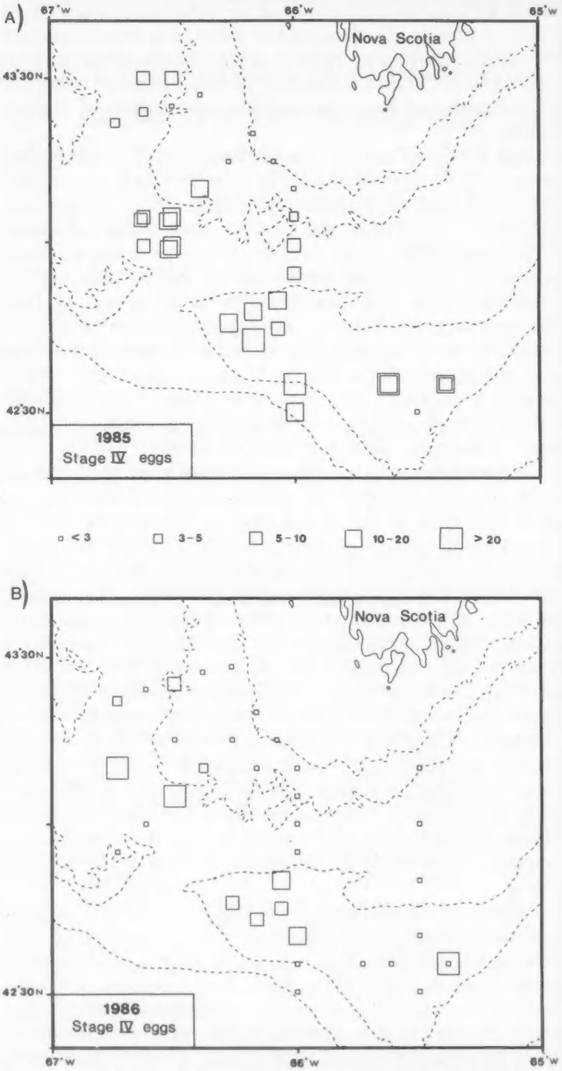

FIG. 2. Distribution of stage IV haddock eggs (number/100 m^3) averaged over the water column from BIONESS collections made during (A) May 1985 and (B) May 1986. Some stations were sampled more than once during the surveys and both values are shown.

Haddock larvae were most frequently encountered at those stations north of Browns Bank during the 1985 survey (Fig. 3). Only 16% of the total number of larvae were collected on the bank. The abundance of haddock larvae was quite low during 1985, with only one station yielding a density greater than 1/100 m^3 (Fig. 3). The average density over the survey area was

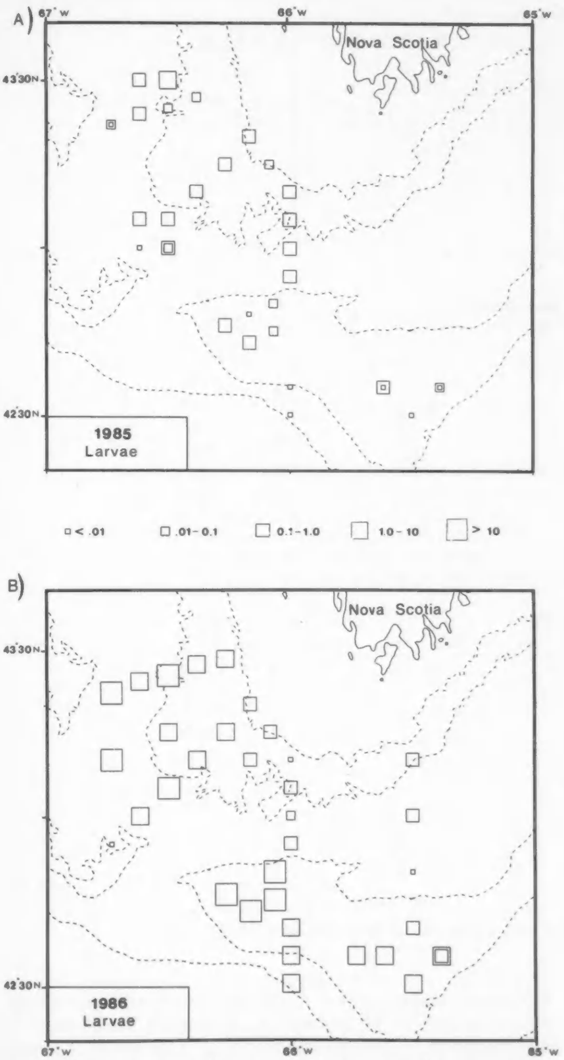

FIG. 3. Distribution of haddock larvae (number/100 m^3) averaged over the water column from BIONESS collections made during (A) May 1985 and (B) May 1986.

0.2 larvae/100 m^3. During May 1986, high concentrations of larvae were encountered on Browns Bank, with 62% of the total number of larvae collected occurring there. The average density of haddock larvae over the survey area was 10/100 m^3 (range 0–112/100 m^3), nearly two orders of magnitude greater than the mean for 1985. In 1986, 65% of the stations yielded densities in excess of 1/100 m^3 (Fig. 3).

It appears that the timing of the survey in relation to the early development of haddock was best suited for the detailed evaluation of the vertical distribution of the egg stage in 1985 and larvae in 1986.

Vertical Distribution

The geometric mean concentration of haddock eggs was calculated for each depth stratum and stage of development (Fig. 4) because egg and larval concentrations at each depth were log-normally distributed. All egg developmental stages of haddock, except the terminal one, declined exponentially with depth in a manner consistent with a previous analysis of discrete depth collections of haddock eggs made on the eastern cap of Browns Bank during May 1984 (Page et al. 1989). Egg stages I–III were largely confined to the upper 20 m during May 1985 (percentage in upper 20 m relative to total collected over all depths: stage I = 76%; stage II = 79%; stage III = 72%). Stage IV haddock eggs exhibited a peak at middepth, with only 41% occurring in the upper 20 m (Fig. 4). The low egg abundance in 1986 lessened our confidence in discerning patterns in the vertical distribution, although stage IV eggs did appear to show a pattern similar to the one observed in 1985 (42% in upper 20 m), and the stage I and II eggs declined exponentially with depth.

Haddock larvae tended to be concentrated at 30 m during the 1986 survey (Fig. 4). The shape of the vertical distribution of larvae was similar to that of the stage IV eggs. The modal size of haddock larvae was 5 mm with a mean of 5.9 mm (range 3–13 mm). Too few larvae were available during 1985 for a meaningful analysis of their vertical distribution.

Hydrographic Conditions

During 1985, temperatures steadily declined from an average of 4.4°C at 5 m to a minimum of 4.1°C at 35 m (Fig. 5). Thereafter, temperatures increased to a maximum of 4.6°C at 65 m. A similar pattern was evident during 1986 except that the average temperature at depth was generally higher by about 1° at all depths (Fig. 5). Salinity decreased monotonically with depth in both years although it was higher at all depths in 1985. The vertical gradient of sigma-*t* was identical between years, increasing linearly with depth, but the intercepts (sigma-*t* at the surface) were different. The linear increase in density was evident at all stations but the slopes differed with a tendency towards decreasing slopes from offshore to nearshore. The higher salinity and lower temperature observed in 1985 resulted in a greater sigma-*t* at all depths in comparison to 1986 (Fig. 5).

Spatial Variation in Haddock Egg Depth Distribution

Thus far we have presented the average or composite picture of the vertical profiles of haddock eggs, larvae, and the physical environment. Now we examine the variance in the depth profile of haddock eggs as a function of changes in the density (sigma-*t*) distribution using, as a conceptual guide, the steady-state vertical distribution model developed by Page et al. (1989). The depth distribution of fish eggs results from the balance between the rate of vertical mixing and the terminal velocity of the eggs. Briefly, the model shows that when the specific gravity of eggs is less than that of the surface water, egg concentration decreases exponentially with depth. When the specific gravity of eggs exceeds that of the surface water, egg concentration profiles will be characterized by a subsurface maximum. The depth of the subsurface maximum is where the egg specific gravity equals the density of the water. An estimate of this depth is the vertical centre of mass (Z_{cm}).

Where egg specific gravity exceeds that of the surface water, depth distribution of the eggs varies as a function of the mean and vertical gradient in density (Fig. 6). The linear slope in density varies by a factor of 4 and the surface sigma-*t* increases from profiles A, B, and C to A′, B′, and C′. For example,

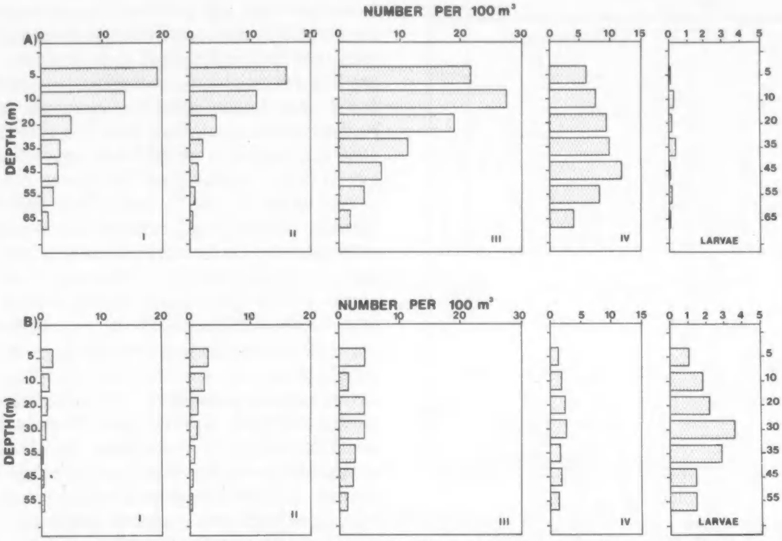

FIG. 4. Depth distribution of haddock eggs (stages I–IV) and larvae averaged over each depth stratum and station in the survey area for (A) May 1985 and (B) May 1986. Values are geometric means.

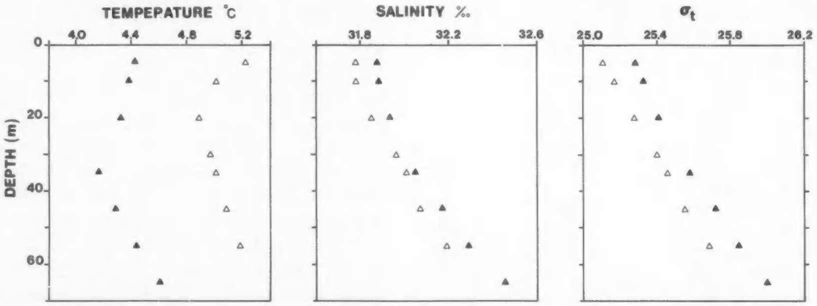

FIG. 5. Depth profile of average temperature, salinity, and sigma-*t* over the survey area during May 1985 (▲) and May 1986 (Δ).

water columns A and A′ have a slope of 0.5 but a different surface sigma-*t* (identical to the situation shown in Fig. 5). The vertical centre of mass of the eggs increases as the slope of sigma-*t* decreases and sigma-*t* at the surface decreases. It also shows that the eggs become more aggregated, i.e. the value of the dispersion index (*s*) increases, with an increase in slope of sigma-*t*.

The data collected in 1985 and 1986 are consistent with the model assumptions and predictions. On average, sigma-*t* increases linearly with depth and the composite depth profiles of egg stages I, II, and III decrease exponentially with depth (Fig. 4 and 5). The depth profile of stage IV eggs exhibits a subsurface maximum (Fig. 4). Each of these features is also consistently exhibited in the individual station profiles for the May 1985 survey, when high egg concentrations were observed (Fig. 2).

A highly significant ($p < 0.001$) positive relationship was found between the vertical dispersion of stage IV haddock eggs (s) and the intensity of stratification (X) (Fig. 7). The equation describing this relationship is

$$s = 1.2145X - 5.43, \qquad R^2 = 0.60, n = 17.$$

At stations exhibiting relatively strong stratification, as was typical of stations on the eastern cap of Browns Bank, stage IV eggs were highly aggregated at middepth. Conversely, haddock eggs showed a more uniform depth distribution under weaker stratification at off-bank locations (Fig. 7). Data from two of the stations (1 and 2 in Fig. 7) exert a strong effect on the significance of the relationship and when both are eliminated reduce the explained variance by 38%.

Given the agreement between the model predictions and observations, it was decided to further examine the spatial variation in the vertical distribution of eggs and density stratification from the 1985 survey. For this analysis we have approximated the depth of the subsurface peak in egg concentrations by using Z_{cm}.

Vertical sections of sigma-*t* for each of the four cross-shelf transects are shown in Fig. 8. Also, Z_{cm} of stage IV eggs is shown for all stations where the sigma-*t* at the maximum sampling depth exceeded 25.5. This cut-off value is close to the specific gravity of stage IV haddock eggs estimated by Page et al. (1989). At stations where this condition did not occur, Z_{cm} is not a good estimator of the depth of neutral buoyancy due to the expected occurrence of peak egg concentrations below the maximum sampling depth.

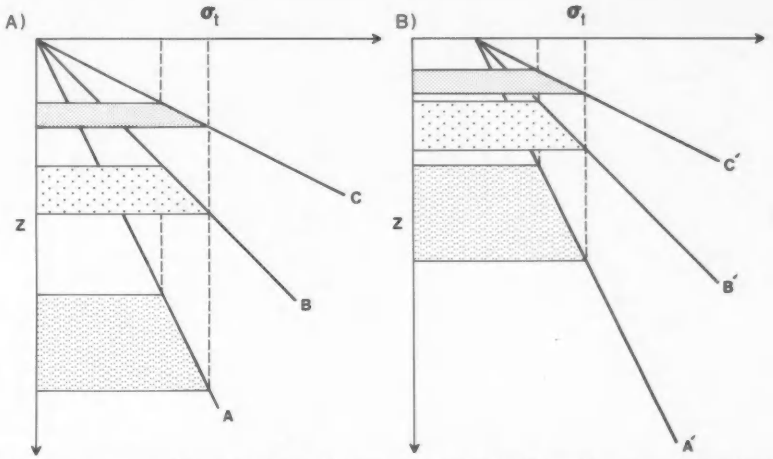

FIG. 6. Conceptual model showing relationship between variation in the intensity of stratification (defined as slope of sigma-*t* versus depth), estimated neutral buoyancy of stage IV haddock eggs (broken vertical lines), and vertical dispersion of stage IV eggs. Note that in Fig. 6A, surface sigma-*t* is lower than in Fig. 6B. See text for detailed explanation.

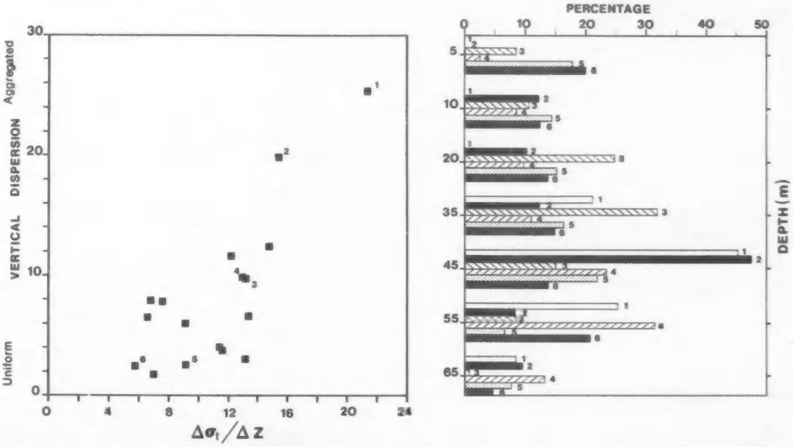

FIG. 7. Relationship between the vertical dispersion of stage IV haddock eggs ($s \times 100$) during May 1985 and stratification intensity (defined as (sigma-*t* at 55 m − sigma-*t* at 5 m)/50 m × 1000). Adjoining panel shows exemplary egg depth profiles at 6 of the 17 stations used to construct the relationship. Location of stations in survey area: 1, D-2; 2, D-3; 3, B-1; 4, C-1; 5, B-2; 6, C-7.

Transect A shows a weakening of the density gradient from offshore to nearshore, with the Z_{cm} for stage IV eggs occurring close to the 25.5 sigma-*t* surface (Fig. 8). The vertical distributions of stage IV eggs were well defined only at stations 1 and 2. The remaining stations along transect A show egg concentration maxima at the maximum sampling depth, suggesting incomplete sampling of the depth range of occurrence of eggs.

The centre of mass of stage IV eggs straddled the depth of the 25.5 isopycnal along transect B (Fig. 9). Between stations 1 and 3 the Z_{cm} of stage IV eggs varied from 43 to 20 m. At stations 4 and 5, where the 25.5 sigma-*t* surface was either absent or below the maximum sampling depth, the peak concentration of eggs occurred at the deepest sampling stratum (Fig. 9). Apparently the occurrence of low-density water in the nearshore results in stage IV haddock eggs sinking or possibly settling on the bottom.

Density stratification from offshore to nearshore tended to weaken along transect C (Fig. 10). Changes in the density stratification were reflected in an aggregated distribution of eggs at middepth at stations 1–5 and a more uniform depth distribution off the bank towards the nearshore (stations 6–8). Also, the centre of mass of stage IV eggs was reasonably well defined by the depth of the 25.5 sigma-*t* surface, with the Z_{cm} of stage IV ranging from 15 to 35 m. Once again the absence of the 25.5 sigma-*t* surface in the nearshore region (station 9) yielded a maximum egg concentration at the deepest sampling stratum (Fig. 10).

The stations sampled along transect D during 1985 were confined to the eastern cap of Browns Bank where the water column was strongly stratified relative to the other sampling locations in the survey area. The centre of mass of stage IV eggs, which ranged from 28 to 45 m, was defined by the depth

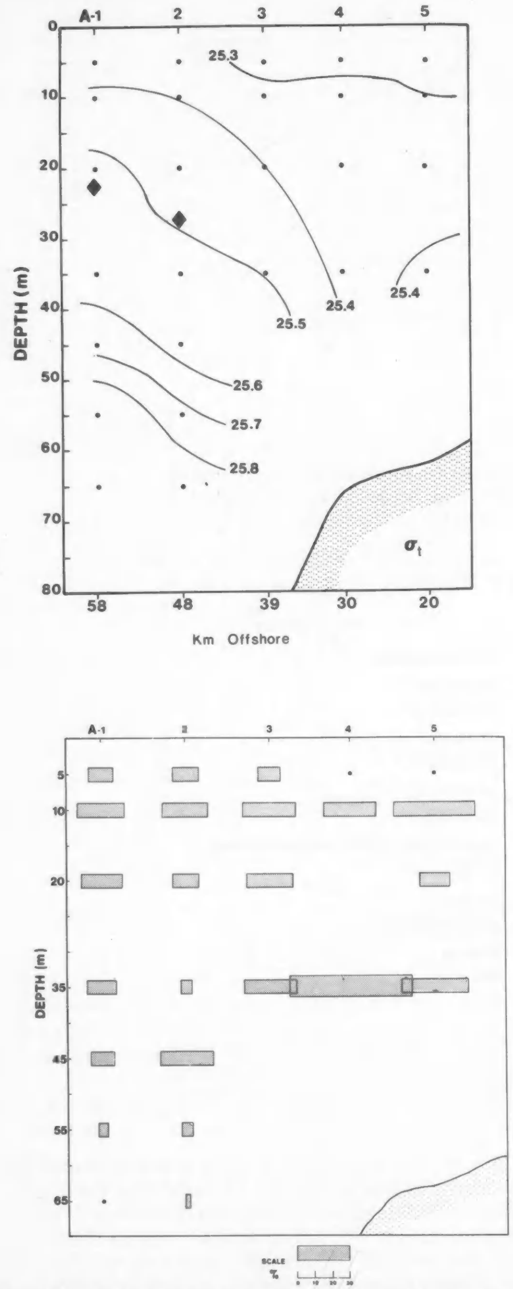

FIG. 8. Vertical section of density (sigma-*t*) for transect A of the May 1985 cruise. Symbol shows depth of centre of mass of stage IV haddock eggs. Lower panel shows proportion of stage IV haddock eggs at depth relative to total collected over all sampling depths. Station positions are indicated along the top of each panel.

of the 25.5–25.6 sigma-*t* surface (Fig. 11). Maximum concentrations of eggs occurred at middepth in response to the strong density stratification.

Collectively, these data are consistent with the hypothesis that stage IV haddock eggs are distributed in relation to their neutral buoyancy. The data also show that the degree of aggregation of eggs over the depth range sampled is influenced by the intensity of stratification and that at the nearshore locations where water less dense than haddock eggs persists, the eggs apparently are most abundant at depths below the maximum sampling depth (and possibly on the bottom). An estimate of the specific gravity of the stage IV eggs is, therefore, given by the average of the sigma-*t* values at each Z_{cm}. For this calculation, only those profiles in which the maximum egg concentration occurred above the maximum sampling depth were included. The average value is 25.58 (95% C.I. 25.53–25.63).

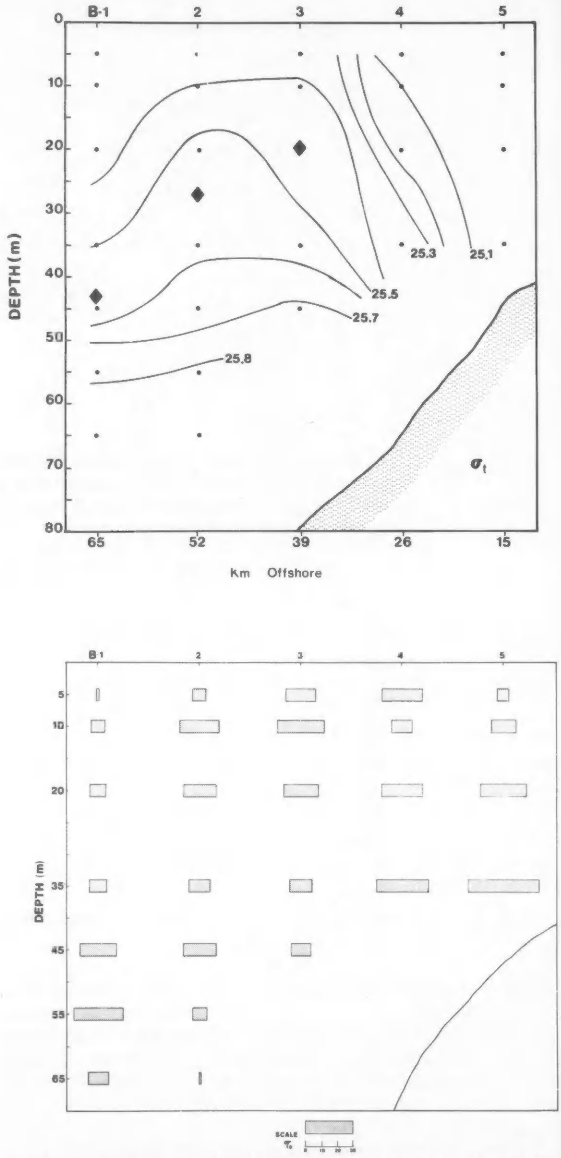

FIG. 9. Vertical cross-section of density (sigma-*t*) for transect B. See legend to Fig. 8 for description.

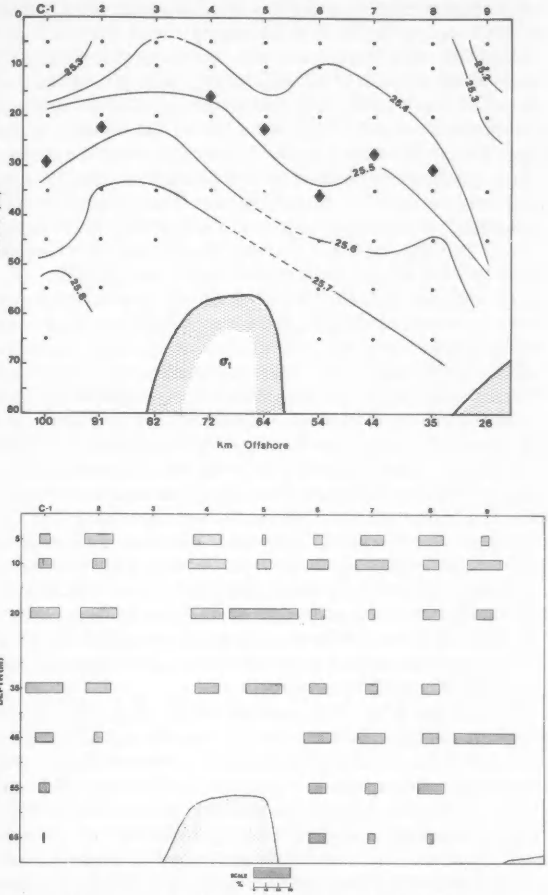

FIG. 10. Vertical cross-section of density (sigma-t) for transect C. See legend to Fig. 8 for description.

Two points should be made here. First, at several offshore stations distributed away from the four transects (Fig. 1) and not shown on Fig. 8–11, Z_{cm} of stage IV eggs was highly variable (range 13–34 m) and the corresponding sigma-t relatively invariant (mean 25.52; 95% C.I. 25.49–25.56), a result entirely consistent with what has been shown thus far. Second, at some stations the centre of mass of stage IV eggs occurred at depths where there were low egg densities. However, the correlation between Z_{cm} and the depth of occurrence of maximum egg density was highly significant ($r = 0.76$, $p < 0.001$).

Vertical Distribution of Haddock Larvae

The centre of mass of haddock larvae during May 1986 was located at a depth of 29 m. No significant differences ($p > 0.05$) were evident between the day and night depth distributions (day: average $Z_{cm} = 28$ m; night: average $Z_{cm} = 31$ m). Disaggregating the data into 1-mm size intervals and recalculating the day and night depth distributions showed no significant differences for any of the size groups evaluated (Fig. 12). These data show that haddock larvae remain at middepth for at least the first 20 d or so after hatching and that the first-feeding larvae (<5 mm) occur within the depth range of the stage IV eggs (Fig. 13). Consequently, the association of haddock larvae with the waters at middepth results from buoyancy changes occurring during the embryonic period.

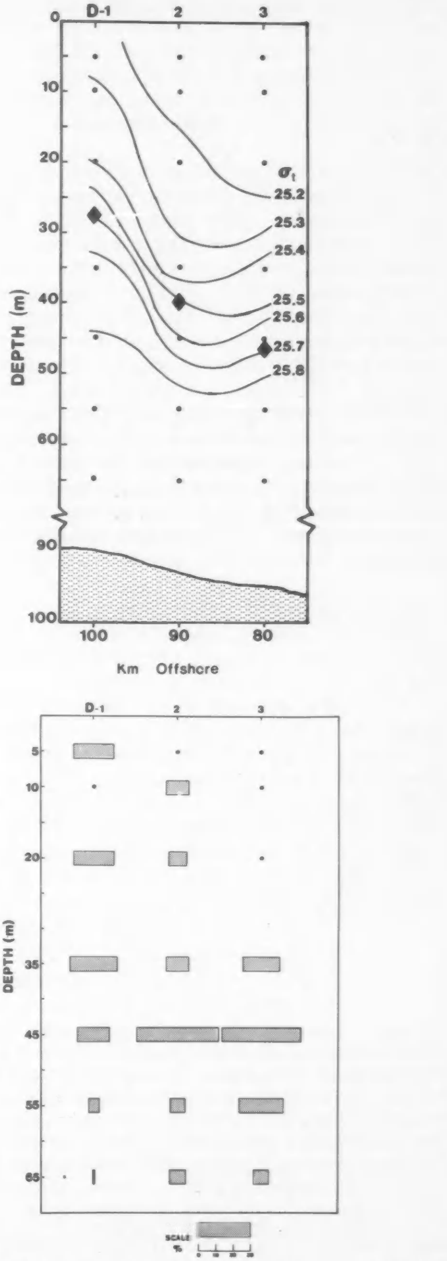

FIG. 11. Vertical cross-section of density (sigma-t) for transect D. See legend to Fig. 8 for description.

Discussion

Our results show that stage IV haddock eggs are distributed in relation to their specific gravity. The Z_{cm} ranged from 13 to

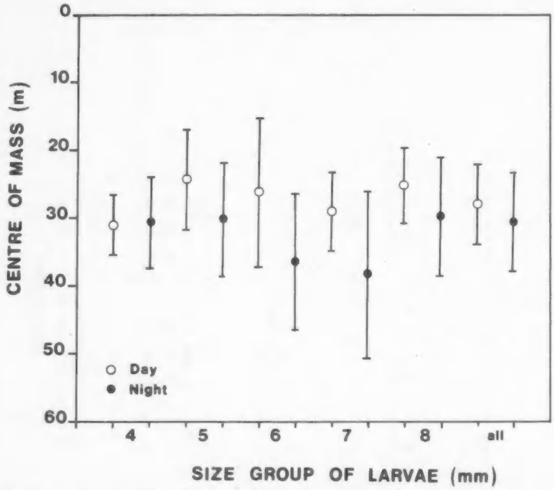

FIG. 12. Average Z_{cm} of five discrete size groups of haddock larvae (all sizes combined also shown) from the May 1986 survey during daytime (0600–1900) and nighttime. Error bars show 95% confidence intervals.

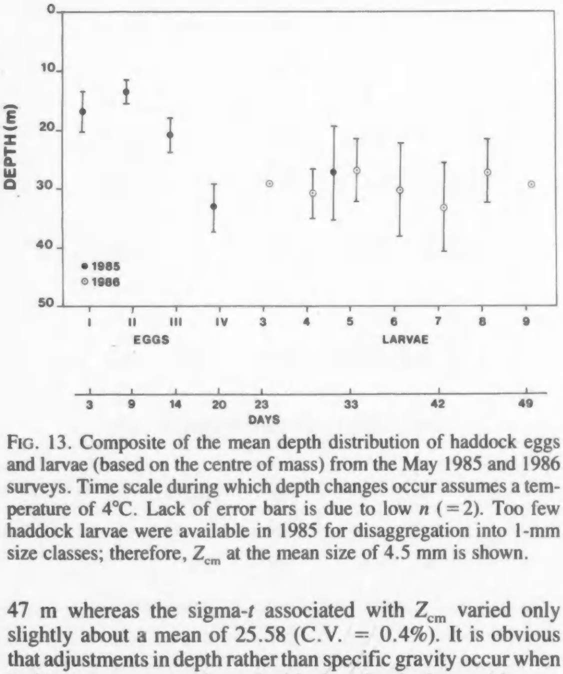

FIG. 13. Composite of the mean depth distribution of haddock eggs and larvae (based on the centre of mass) from the May 1985 and 1986 surveys. Time scale during which depth changes occur assumes a temperature of 4°C. Lack of error bars is due to low n (=2). Too few haddock larvae were available in 1985 for disaggregation into 1-mm size classes; therefore, Z_{cm} at the mean size of 4.5 mm is shown.

47 m whereas the sigma-t associated with Z_{cm} varied only slightly about a mean of 25.58 (C.V. = 0.4%). It is obvious that adjustments in depth rather than specific gravity occur when haddock eggs are confronted with changing hydrographic conditions. In this respect, haddock eggs are similar to those of Atlantic halibut (Haug et al. 1986) showing depth distributions, both the mean and variance, determined by the interaction of their neutral buoyancy with the hydrographic structure of the water column. This has obvious consequences in terms of survey design, the influence of currents on distribution, and conditions at first feeding.

Haddock eggs achieved a higher specific gravity with age as evidenced by their increasing depth distribution, ranging from a minimum average centre of mass of 14 m for stage II eggs (95% C.I. 12–16 m) to 33 m for stage IV eggs (95% C.I. 29–37 m). This result is consistent with several previous studies of the depth distribution of pelagic fish eggs (see the introduction for examples). The net result of ontogenetic changes in depth distribution during the embryonic period for haddock is the establishment of newly hatched larvae at intermediate depths. The coincidence between the centre of mass of stage IV eggs and larvae supports this claim (Fig. 12). This temporal pattern of residence at increasing depths could serve to reduce dispersion of the eggs into areas outside the normal distributional range by reducing the influence of wind-driven currents associated with the upper mixed layer. In this sense, continuity between the distribution of haddock eggs and larvae with their spawning location is achieved as a result of events occurring during the embryonic period. Our results are analogous to those of Henri et al. (1985) who have shown that ontogenetic changes in specific gravity of herring larvae, from a maximum at hatching to a minimum during the post-yolk sac stages, contribute to their retention and aggregation in the St. Lawrence estuary. Similarly, Caddy and Iles (1973) observed dense concentrations of herring larvae within 1 m of the bottom shortly after hatching on Georges Bank which would reduce their rate of dispersion, relative to other positions in the water column, from this tidally energetic region. Also, Frank and Carscadden (1989) have hypothesized that buoyancy changes enable malnourished capelin (*Mallotus villosus*) larvae to ascend passively through a strong pycnocline from the bottom waters to the food-rich surface layer shortly after hatching.

The physical factors concentrating haddock eggs at middepth may have similar effects on prey for first-feeding larvae. This would result in a favourable feeding environment for larvae and is consistent with the scenario developed by Buckley and Lough (1987) for growth and survival of haddock larvae on Georges Bank. Haddock larvae inhabiting stratified sites on Georges Bank showed superior condition and growth relative to larvae at well-mixed sites. Prey concentrations up to 30-fold greater at the stratified sites were believed to be responsible for the difference in condition and growth (Buckley and Lough 1987). It is difficult to distinguish the effects of stratification and prey concentration on larval growth, although Lough (1984) hypothesized that they were directly related. Published studies from other geographic regions have demonstrated a positive effect of stratification on the concentration of potential prey for larvae (Brandt and Wadley 1981; Bakun and Parrish 1982; Tilseth and Ellertsen 1984; Petersen and Ausubel 1984). If this is a general phenomenon, we would expect to find a result consistent with Buckley and Lough (1987) within the distributional range of haddock in southwestern Nova Scotia. Recent results tend to support their findings: interstation variability in the mean condition of haddock larvae from the 1986 May survey was explained by stratification intensity, with high larval condition being associated with stratified waters (Frank and McRuer 1989).

Previous broad-scale studies of the vertical distribution of haddock eggs in the Northwest Atlantic are limited to Georges Bank (Colton 1965). The major findings there were that the vertical distribution of haddock eggs did not vary appreciably in time or space and that nearly all developmental stages occurred in the upper 20 mm of the water column, with egg abundance declining with increasing depth. Based on such information, Colton (1965) argued for sampling of a limited depth stratum to obtain reliable estimates of abundance over broad geographical areas. Our results conflict strongly with those of Colton (1965), probably due to the coarse egg-staging system and low-resolution vertical sampling he employed. Nevertheless, we would argue against any recommendation for sampling a limited depth stratum given the strong effect of hydrographic factors on the mean depth and variance of haddock eggs seen in our study. Furthermore, a single profile of gadid eggs (mainly haddock) from Georges Bank during April 1981, when the water column was well mixed, showed egg concentrations *increasing* with depth to a maximum near the bottom and mean depth of about 40 m (Lough 1984).

The similarity in day and night depth distributions of haddock larvae <9 mm in the Browns Bank region (Fig. 12) is also evident among the later larval and pelagic juvenile stages of haddock on Georges Bank (Miller et al. 1963; Colton 1965; Perry and Neilson 1988). Miller et al. (1963) showed that greater than 80% of the haddock larvae ranging in size from 8 to 20 mm coincided with the thermocline (10–40 m) during May 1958. The mean depth of larvae at three sampling sites during daytime and nighttime was 28 and 22 m, 18 and 23 m, and 25 and 22 m, respectively. Stability in the depth distributions persists well into the juvenile stage. Greater than 75% of juvenile haddock (size range 27–124 mm) occurred between depths of 10 and 40 m during summer surveys of Georges Bank in 1957 and 1958 (Colton 1965). This depth range included the thermocline, and the mean depth of occurrence in each year was 28 and 33 m. The recent results of a survey conducted in June 1985 (Perry and Neilson 1988) are in general agreement with previous studies, i.e. juvenile haddock showed no evidence of diel variation in depth distribution with a mean depth ranging between 20 and 40 m coincident with the thermocline. Obviously, some explanation other than vertical migration will be required to explain the temporal persistence in some years of haddock larvae on Browns and Georges Bank, and it is possible that the physical features associated with the spawning location may act to minimize dispersion. In this regard it is worth noting that cross-shelf transport is likely to be reduced for residents of the pycnocline, a region typified by low cross-shelf transport and at approximately the same depth as the thermocline (Winant and Olson 1976; Kundu 1977).

Association with specific water masses during spawning imparts unique buoyancy characteristics to the eggs (Solemdal 1967, 1971, 1973). Haddock show an affinity for the relatively warm (>22°C), high-salinity slope waters off the southwestern Grand Banks and are associated with intrusions of slope water onto the shelf during the spawning period (Templeman and Hodder 1965). No observations like this have been made in other geographic areas although subsurface intrusions are an important feature on the Scotian Shelf that contribute in significant ways to the heat and salt budget of the shelf (Smith 1978; Herman and Denman 1979). In the case of Browns Bank haddock, successful reproduction would not be expected to occur where the density of the bottom waters was less than 25.5–25.6 (i.e. the density required to maintain stage IV haddock eggs suspended in the water column).

Year class strength of cod in the brackish Baltic Sea is strongly influenced by the hydrographic conditions of the bottom waters acting during the embryonic period (Grauman 1973). The hydrographic regime of the near-bottom layer changes considerably from year to year due to variation in the influx of North Sea waters. Cod eggs experience high mortality rates in years of below-average salinity due to the settlement of eggs on the oxygen-poor bottom (Grauman 1973). This relationship is similar to the one previously documented by Johansen (1927) who showed that plaice recruitment and salinity anomalies covaried in the Baltic Sea. He suggested that plaice eggs sinking to the bottom were rapidly consumed. Regardless of the exact cause of death, it is generally believed that the mortality of pelagic eggs developing on the bottom is very great (Solemdal 1967).

Haddock eggs originating from Browns Bank would probably fail to hatch in the nearshore waters off southwestern Nova Scotia because of the low-density water that persists in the region. Such a mechanism would prevent colonization of the nearshore waters from offshore spawning and thereby serve to define the distributional limits of the early life stages. Even if hatching were to occur in the nearshore, the persistent, weak stratification typical of the region would impose another obstacle to larval survival in the same sense that it does on the shoal waters of Georges Bank (Buckley and Lough 1987). Also, previous observations of the broad-scale distribution of haddock eggs in the region are consistent with the suggested mechanism. Koslow et al. (1985) found that sampling stations without haddock eggs during the spring of 1983 were predominantly on the periphery of the survey area in southwestern Nova Scotia. This lead to the appearance of an increasingly clumped and aggregated egg distribution with time (development) centred on Browns Bank.

On the other hand, a close relative of haddock, the cod, occurs in waters having a wide range of salinities with no simple definition of the hydrographic conditions associated with spawning (Wise 1961). There are nearly twice as many cod stocks as haddock stocks in the Northwest Atlantic due to the many local populations spawning in coastal waters. Also, larval cod are less sensitive to stratification than haddock larvae and appear to grow well in well-mixed areas on Georges Bank (Buckley and Lough 1987). Sinclair (1988) has suggested that "there may be very subtle differences in the behaviour of the larvae that allow cod populations to be more numerous." It is entirely possible that one of the reasons underlying this fact is differences in the specific gravity of their eggs and the ecological consequences that result from them.

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References

BAKUN, A., AND R. H. PARRISH. 1982. Turbulence, transport, and pelagic fish in the California and Peru current systems. Calif. Coop. Oceanic Fish. Invest. 23: 99–112.

BOLZ, G. R., AND R. G. LOUGH. 1984. Retention of ichthyoplankton in the Georges Bank region during the autumn–winter seasons, 1971–77. J. Northwest Atl. Fish. Sci. 5: 33–45.

BRANDT, S. B., AND V. A. WADLEY. 1981. Thermal fronts and zoogeographic barriers in marine and freshwater systems. Proc. Ecol. Soc. Aust. 11: 13–26.

Buckley, L. J., and R. G. Lough. 1987. Recent growth, biochemical compostion, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44: 14–25.

Caddy, J. F., and T. D. Iles. 1973. Underwater observations on herring spawning grounds on Georges Bank. ICNAF Res. Bull. 10: 131–139.

Colton, J. B., Jr. 1965. The distribution and behaviour of pelagic and early demersal stages of haddock in relation to sampling techniques. ICNAF Spec. Publ. No. 6: 317–333.

Colton, J. B. Jr., W. G. Smith, A. W. Kendall, P. L. Berrien, and M. P. Fahay. 1979. Principal spawning areas and time of marine fishes, Cape Sable to Cape Hatteras. Fish. Bull. 76: 911–915.

Coombs, S. H., C. A. Fosh, and M. A. Keen. 1985. The buoyancy and vertical distribution of eggs of sprat (*Sprattus sprattus*) and pilchard (*Sardina pilchardus*). J. Mar. Biol. Assoc. U.K. 65: 461–474.

Craik, J. C. A., and S. M. Harvey. 1987. The causes of buoyancy in eggs of marine teleosts. J. Mar. Biol. Assoc. U.K. 67: 169–182.

Fitzpatrick, C., and R. J. Miller. 1979. Review of spawning times and locations for some commercial finfish on the Newfoundland and Labrador coasts. Fish. Mar. Serv. Tech. Rep. 905: v + 14 p.

Fournier, R. O., M. Van Det, N. B. Hargreaves, J. S. Wilson, T. A. Clair, and R. Ernst. 1984. Physical factors controlling summer distribution of chlorophyll *a* off southwestern Nova Scotia. Limnol. Oceanogr. 29: 517–526.

Frank, K. T., and J. E. Carscadden. 1989. Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic. J. Cons. Int. Explor. Mer 45: 146–164.

Frank, K. T., and J. K. McRuer. 1989. Nutritional status of field-collected haddock (*Melanogrammus aeglefinus*) larvae from southwestern Nova Scotia: an assessment based upon morphometric and vertical distribution data. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): (This issue).

Grauman, G. B. 1973. Investigations of factors influencing fluctuations in abundance of Baltic cod. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 73–76.

Grosslein, M. D., and R. C. Hennemuth. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 77–88.

Haug, T., E. Kjorsvik, and P. Solemdal. 1986. Influence of some physical and biological factors on the density and vertical distribution of Atlantic halibut *Hippoglossus hippoglossus* eggs. Mar. Ecol. Prog. Ser. 33: 207–216.

Hempel, G. 1979. Early life history of marine fish: the egg stage. University of Washington Press, Seattle and London. 70 p.

Henri, M., J. J. Dodson, and H. Powles. 1985. Spatial configurations of young herring (*Clupea harengus harengus*) larvae in the St. Lawrence estuary: importance of biological and physical factors. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 91–104.

Herman, A. W., and K. L. Denman. 1979. Intrusions and vertical mixing at the shelf/slope water front south of Nova Scotia. J. Fish. Res. Board Can. 36: 1445–1453.

Johansen, A. C. 1927. On the fluctuations in the quantity of young fry among plaice and certain other species of fish, and causes of the same. Rep. Dan. Biol. Stn. 33: 1–16.

Kanoh, Y. 1955. On the buoyancy of the egg of Alaska pollack. Jpn. J. Ichthyol. 3: 238–246.

Koslow, J. A., S. Brault, J. Dugas, and F. Page. 1985. Anatomy of an apparent year-class failure: the early life history of the 1983 Browns Bank haddock *Melanogrammus aeglefinus*. Trans. Am. Fish. Soc. 114: 478–489.

Kundu, P. K. 1977. On the importance of friction in two typical continental waters: off Oregon and Spanish Sahara, p. 187–207. *In* J. Nihoul [ed.] Bottom turbulence. Proc. 8th Liege Colloq. Ocean Hydrodyn. Elsevier, New York, NY.

Lough, R. G. 1984. Larval fish trophodynamic studies on Georges Bank: sampling strategy and initial results, p. 395–434. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flodevigen rapportser 1.

Markle, D. F., and L.-A. Frost. 1985. Comparative morphology, seasonality, and a key to planktonic fish eggs from the Nova Scotian shelf. Can. J. Zool. 63: 246–257.

Miller, D., J. B. Colton, and R. R. Marak. 1963. A study of the vertical distribution of larval haddock. J. Cons. Int. Explor. Mer 178: 144–149.

Mork, J., P. Solemdal, and G. Sundnes. 1983. Identification of marine fish eggs: a biochemical genetics approach. Can. J. Fish. Aquat. Sci. 40: 361–369.

Needler, A. W. H. 1929. Studies on the life history of the haddock (*Melanogrammus aeglefinus* L.). Contrib. Can. Biol. Fish. N.S. 4: 267–285.

Nishiyama, T., K. Hirano, and T. Haryu. 1984. The early life history and feeding habits of larval walleye pollock *Theragra chalcogramma* (Pallas) in the southeast Bering Sea. Int. North Pac. Fish. Comm. Bull. 45: 177–227.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 183: 27–40.

Page, F. H., K. T. Frank, and K. Thompson. 1989. Stage-dependent vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs in a stratified water column: model and observations. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): (This issue).

Perry, R. I., and J. D. Neilson. 1988. Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. Mar. Ecol. Prog. Ser. 49: 199–214.

Peterson, W. T., and S. J. Ausubel. 1984. Diets and selective feeding by larvae of Atlantic mackerel *Scomber scombrus* on zooplankton. Mar. Ecol. Prog. Ser. 17: 65–75.

Riis-Vestergaard, J. 1983. Water and salt balance of halibut eggs and larvae (*Hippoglossus hippoglossus*). Mar. Biol. 70: 135–139.

Sameoto, D. D., L. O. Jaroszynski, and W. B. Fraser. 1980. BIONESS, a new design in multiple net zooplankton samplers. Can. J. Fish. Aquat. Sci. 37: 722–724.

Scott, J. S. 1983. Inferred spawning areas and seasons for groundfishes on the Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 1219: iii + 14 p.

Scott, W. B., and M. G. Scott. 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219: 731 p.

Sherman, K., W. Smith, W. Morse, M. Berman, J. Green, and L. Ejsymont. 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18: 1–19.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle, WA. 252 p.

Sinclair, M., and T. D. Iles. 1988. Population richness of marine fish species. Aquat. Living Resour. 1: 71–83.

Smith, P. C. 1978. Low-frequency fluxes of momentum, heat, salt, and nutrients at the edge of the Scotian Shelf. J. Geophys. Res. 83: 4079–4096.

1983. The mean and seasonal circulation off southwest Nova Scotia. J. Phys. Oceanogr. 13: 1034–1054.

1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

Solemdal, P. 1967. The effect of salinity on buoyancy, size and development of flounder eggs. Sarsia 29: 431–442.

1971. Prespawning flounders transferred to different salinities and the effects on their eggs. Vie Milieu Suppl. 22: 409–423.

1973. Transfer of Baltic flatfish to a marine environment and the long term effects on reproduction. Oikos Suppl. 15: 268–276.

Sundnes, G., H. Leivestad, and O. Iversen. 1965. Buoyancy determination of eggs from the cod (*Gadus morhua* L.). J. Cons. Int. Explor. Mer 29: 249–252.

Templeman, W., and V. M. Hodder. 1965. Distribution of haddock on the Grand Bank in relation to season, depth and temperature. ICNAF Spec. Publ. 6: 171–187.

Tilseth, S., and B. Ellertsen. 1984. The detection and distribution of larval Arcto–Norwegian cod, *Gadus morhua*, food organisms by an in situ particle counter. Fish. Bull. 82: 141–156.

UNESCO. 1981. Background papers and supporting data on the international equation of stage of seawater 1980. UNESCO Tech. Pap. Mar. Sci. 38: 3–7.

Walford, L. A. 1938. Effect of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank. U.S. Bur. Fish. Bull. 49: 1–73.

Ware, D. M., and T. H. Lambert. 1985. Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 42: 577–592.

Winant, C. S., and J. R. Olson. 1976. The vertical structure of coastal currents. Deep-Sea Res. 23: 925–936.

Wise, J. P. 1961. Synopsis of biological data on cod *Gadus morhua* L. FAO Fish. Biol. Synop. No. 21: 28 p.

A Drift–Retention Dichotomy for Larval Haddock (*Melanogrammus aeglefinus*) Spawned on Browns Bank[1]

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This study was designed to assess the dispersal of haddock (*Melanogrammus aeglefinus*) larvae from their Browns Bank spawning site in terms of either drift or retention mechanisms. Larvae were collected in comprehensive surveys of southwestern Nova Scotia conducted at monthly intervals through the winter–spring of 1985. To avoid any confounding of larval displacement patterns by the numerically dominant young larvae, all spatial analyses were structured by age through otolith microstructure techniques. The results of a trend surface analysis indicated that both drift and retention processes operated in concert to split and disperse the larval population. Retention was probably physically based, through the action of a "leaky" gyre around Browns Bank. Although similar processes are believed to have influenced the distribution of Browns Bank cod (*Gadus morhua*) larvae, the interspecific difference in spawning time, coupled with the apparent instability of the gyre, produced a different balance between transported and retained larvae. A drift–retention dichotomy for Browns Bank ichthyoplankton has implications for both recruitment and stock structure studies.

Cette étude visait à évaluer la dispersion des larves d'aiglefin (*Melanogrammus aeglefinus*) depuis leur aire de fraye du banc Browns en fonction soit de la dérivation ou des mécanismes de rétention. Des larves ont été recueillies au cours de levés exhaustifs mensuels effectués dans le sud-ouest de la Nouvelle-Écosse au cours du printemps et de l'hiver 1985. Afin de ne pas confondre les modes de déplacement des larves à cause du nombre dominant de jeunes larves, toutes les analyses spatiales ont été structurées par âge au moyen de techniques d'évaluation de la microstructure de l'otolithe. Les résultats d'une analyse superficielle de tendances révèlent que les deux processus de dérivation et de rétention entrent en jeu de concert pour séparer et disperser les populations larvaires. La rétention est probablement d'origine physique, causée par l'action du tourbillon « irrégulier » dans le banc Browns. Bien que des processus semblables pourraient avoir influencé la répartition des larves de morue (*Gadus morhua*) dans le banc Browns, la différence entre les espèces pendant le temps de la fraye, couplée à l'instabilité apparente du tourbillon, a produit un équilibre différent entre les larves transportées et les larves retenues. Une dichotomie dérivation–rétention pour l'ichthyoplancton du banc Browns a des implications tant pour les études sur le recrutement que pour celles sur la structure des stocks.

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Larval drift to a juvenile "nursery area," with a subsequent return migration of adults to spawn, describes the well-known "migration triangle" of Harden-Jones (1968) and provides the basis for a widely accepted hypothesis concerning variability in marine fish production (Cushing 1972). In instances where the spawning site and the subsequent centre of juvenile abundance were widely separated, and particularly where discrete larval cohorts were monitored along their drift path, interpretations other than that of advective drift are difficult to support (e.g. Lear and Green 1982; Fortier and Leggett 1983; Ellertsen et al. 1984; Lockwood and Lucassen 1984; Ouellet and Dodson 1985; Smith and Morse 1985; Cushing 1986; Jahn and Lavenberg 1986; Power 1986; Kendall et al. 1987). However, there are a number of systems in which the advection of ichthyoplankton, particularly larvae, is restricted or absent, even in the presence of directed residual currents (Iles and Sinclair 1982). Retention is reported to have been associated most often with physical, particularly tidal, features of the circulation, but vertical movements of larvae have also been implicated (Fortier and Leggett 1983; McCleave et al. 1987; Sinclair and Iles 1988). Despite reports of supporting evidence among several species (Gagné and O'Boyle 1984; O'Boyle et al. 1984; Smith and Morse 1985; Sinclair and Iles 1988), the retention hypothesis has yet to be rigorously tested in species other than Atlantic herring (*Clupea harengus*).

Browns Bank is an appropriate test site for the retention hypothesis, since controversy concerning the importance of retention to the progeny of the resident haddock (*Melanogrammus aeglefinus*) stock already exists. Grosslein and Hennemuth (1973) interpreted captures of settled young-of-the-year haddock, stretching from Browns Bank to the mouth of the Bay of Fundy, as evidence of advective drift. In contrast, O'Boyle et al. (1984) interpreted the spatial coincidence of haddock eggs and larvae on the bank as the first demonstration of retention in this species. Unfortunately, both of these interpretations were confounded by the broad temporal and spatial scales of sampling, the inability to follow discrete larval cohorts, and the aggregation of larvae of all sizes and ages into a single class.

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As noted by Cushing (1986), coincidence of eggs and young larvae may occur even in the presence of drift; any displacement of the older larvae would almost certainly be masked by the numerically dominant younger larvae, which by definition would be in closer proximity to the spawning site. Accordingly, a proper test of the retention hypothesis in this system requires an age-structured analysis of the larval distribution data.

In this paper, we use the results of five synoptic surveys to assess the age-structured spatial distribution of haddock larvae in and around the Browns Bank spawning site. The objective is to quantify the change in larval distribution as a function of larval age and to discuss the findings in the context of the drift–retention controversy: if passive drift is present, larval displacement from the spawning site should increase with age in a direction and at a rate consistent with the residual currents.

Materials and Methods

Haddock larvae were collected in five different cruises over a fixed survey grid as part of the Fisheries Ecology Program (FEP) ichthyoplankton survey. The survey encompassed 97 stations to the south, east, and west of Nova Scotia, down to and including portions of Georges Bank (Fig. 1). Collections were made monthly between February and June 1985, although weather restricted grid coverage on some cruises (Table 1). Each station was sampled with paired, 61-cm bongo nets fitted with 333-μm Nitex mesh and mouth-mounted flowmeters. Tows were made obliquely to within 5 m of the bottom (to a maximum depth of 200 m) and immediately replicated. Full sampling details and cruise-by-cruise station locations are documented elsewhere (Hurley and Campana 1989).

Ichthyplankton samples were preserved and processed as described elsewhere (Campana and Hurley 1989). Since otolith microstructure examination is the most effective and precise age determination tool available for young fish (Pannella 1971; Brothers et al. 1976; reviewed by Campana and Neilson 1985), its use was appropriate in this study. Both pairs of sagittal and lapillar otoliths were removed, mounted individually, and prepared according to standard techniques (Campana and Neilson 1985). All larvae, except those damaged by preservation, were aged. Microstructural interpretations were not independently validated with known-age larvae, but were assumed to be comparable with the morphologically similar (and validated) cod (*Gadus morhua*) otolith (Campana 1989). Thus, daily growth increment counts of the lapillus (plus 1, corresponding to the presumed age at hatch check formation) were taken to accu-

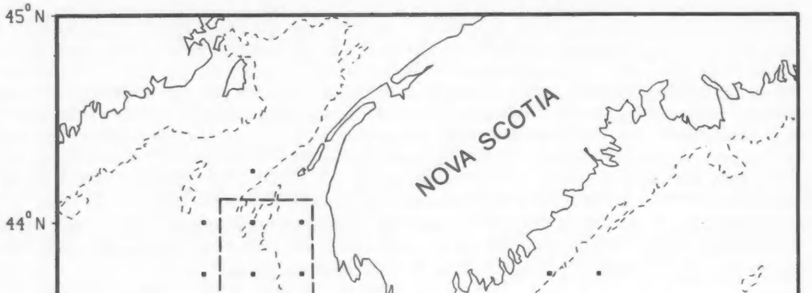

FIG. 1. Study area showing collection stations in reference to the 100-m contour. Browns Bank has been delimited by a solid line. The stations sampled in the May and June cruises are delimited by the broken line.

TABLE 1. Summary of cruises represented in this study.

Cruise	Date (1985)	No. of stations sampled	No. of stations with larvae	No. of larvae	No. of larvae aged
H130	February 4–22	93	0	0	0
H132	March 11–29	49	9	13	7
H133	April 6–17	90	29	53	43
H135	May 6–16	57	31	436	246
H137	June 3–14	59	44	974	881

rately represent the age of the larvae. Ages were probably underestimated by 2–3 d due to the presence of daily increments too narrow to resolve by light microscopy (Campana 1989), but this level of bias was considered both acceptable and unavoidable.

All spatial analyses of the larvae were based upon the age-structured mean number of larvae per square metre of ocean surface. Larval ages were subsequently categorized by 10-d intervals, with the oldest larvae categorized as a plus group (51 + d). The oldest larvae were categorized as 31 + d for the trend surface model. Subsequent stages of data preparation are described elsewhere (Campana et al. 1989).

Trend Surface Analysis

Trend surface analysis is a form of polynomial regression suited to modelling spatial gradients in distributional data (Cliff and Ord 1981; Ripley 1982). In this study, its use simplified the interpretation of the complex, multidimensional age-structured larval distribution data. Several formulations are possible; this study defined the spatial coordinates of latitude (x_{1i}) and longitude (x_{2i}) for the ith sample site as covariates in the following polynomial:

$$(1) \quad \mu_i = \sum_{s=0}^{p} \sum_{r=0}^{q} \beta_{rs} x_{1i}^{r} x_{2i}^{s}$$

where $p + q \leqslant k$ denotes the highest order polynomial terms. Conceptually, trend surface analysis can be envisioned as the topological, or planar, version of a simple, least squares regression. Continuing the analogy, the β parameter in Equation (1) is the slope of the regression, and the two x variables correspond to the two dimensions of the plane. The dependent variable is, of course, larval abundance. The most difficult components to conceptualize are the higher order polynomial terms. These introduce curvilinear gradients into the trends in larval abundance. For example, while a first-order model would allow a linear gradient in abundance to be modelled (e.g. high abundance in the south to low in the north), a second-order (quadratic) model could be used to detect a localized centre of abundance (a dome-shaped abundance pattern), and a cubic model, two centres. Again, the analogy to simple regressions applies, where a simple regression model would be used to fit a straight line, a quadratic model for a parabola, etc. An example of first-, second-, and third-order trend surface models fitted to simulated data is presented in Fig. 2. Trend surface models do not incorporate a spatially dependent covariance structure and therefore are most appropriate for use when external forces (i.e. currents), rather than interindividual interactions, dominate the data. In this study, correlogram tests (Cliff and Ord 1981) indicated that there was no evidence for spatial autocorrelation, either among the observed larval numbers at age or in the model residuals.

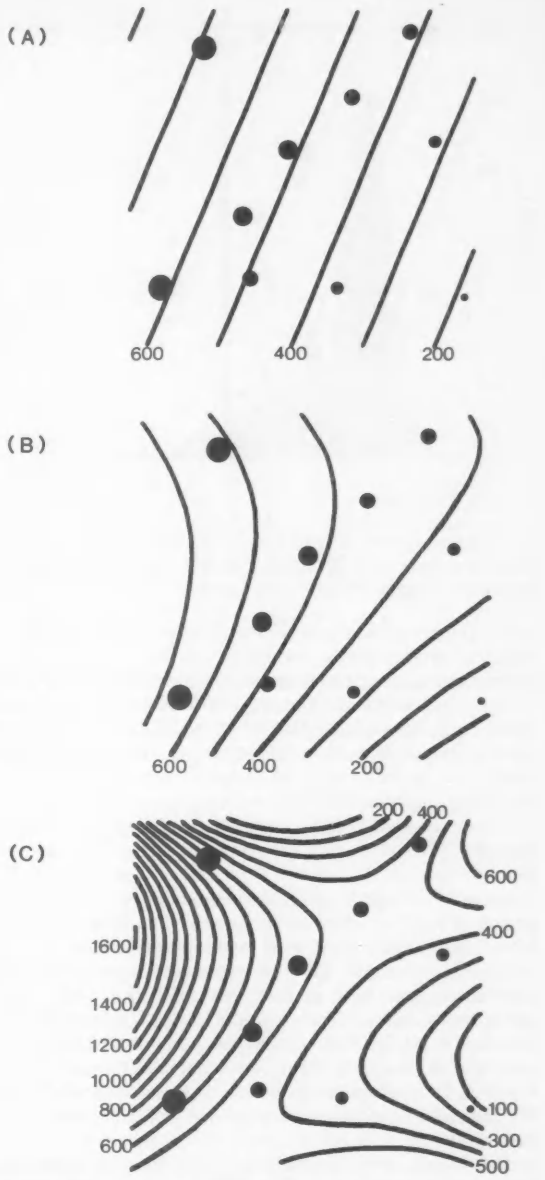

FIG. 2. Example of the abundance contours that would result from the fit of three different trend surface models to a single set of simulated data (modified from Ripley (1982, p. 31–33) with permission of the publisher). (A) First-order model; (B) second-order (quadratic) model; (C) third-order (cubic) model.

In this study, second- and third-order trend surface models were used to allow broad, curvilinear trends in haddock larval abundance to be described. Since station coordinates differed slightly among cruises (despite the fixed survey grid), a standard location was used for each station across cruises. Station coordinates were centred prior to entry into the model. Similarities among age categories and cruises were not assumed: spatial terms were nested within each age category, and ages were nested within cruise. Since the variances were propor-

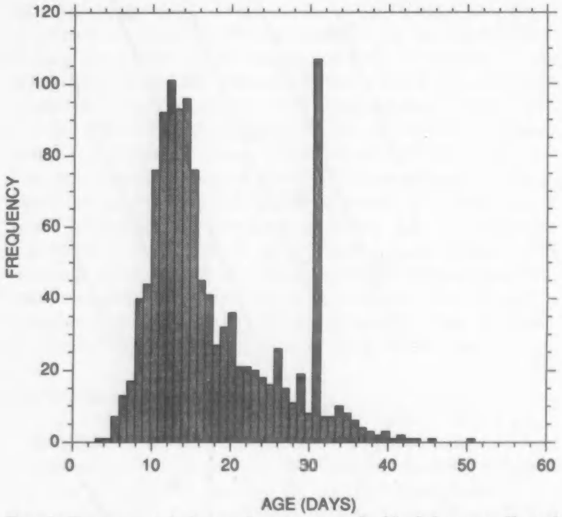

FIG. 3. Frequency of observed ages among haddock larvae collected on five cruises in 1985. The peak at 31 d is largely due to the catch at a single station in the June (H137) cruise.

tional to the means, a generalized Poisson distribution for the response variable was also assumed, with $E[y_i] = \exp(\mu_i)$. The exponential was used to insure that the predicted values were ≥ 0 as expected for the Poisson distribution. Parameter estimates were obtained using iteratively reweighted least squares with the computer package GLIM (Payne 1986). Models were selected using the analysis of deviance approach discussed in McCullagh and Nelder (1983).

Results

A total of 1476 haddock larvae were collected during the five cruises (Table 1), with catches at individual stations ranging from 0 to 171. No larvae were captured in February. Over the remaining cruises, 44% of the stations produced larvae. The age composition of the samples differed both among cruises and among samples (Kruskal–Wallis, $P < 0.01$), with the June cruise (H137) contributing significantly more of the older larvae. Overall, the range of ages spanned 3–51 d, with larvae less than 29 d old making up 86% of the collection (Fig. 3). The mean age of all larvae sampled was 17.5 d (the median age was 15 d).

The relative abundance and spatial distribution of each age category are presented in Fig. 4 although the catches in the March cruise (H132) were too few to present. Both the April (H133) and the May (H135) cruises showed the same general pattern of distribution, with centres of abundance on and to the north–northwest of Browns Bank. Few larvae were found to the east or west of the bank, or in the waters between Browns and Georges banks. In contrast, substantial concentrations of larvae were captured in these latter areas in the June cruise (H137), particularly to the east on Baccaro Bank. Larvae were occasionally found on Georges Bank as well, but in much smaller numbers.

The larval age composition in each region differed slightly among cruises (Fig. 4). Browns Bank and the region immediately north of it (along the 100-m contour) were consistently characterized by a large proportion of larvae less than 20 d old, with significant but lesser proportions of older larvae. The age compositions of regions to the northwest of Browns Bank were generally skewed to the right, indicating an older age distribution. The regions east of Browns Bank were virtually devoid of larvae in all cruises but that of June, but in the latter, a high proportion of both young (<30 d) and old (31–40 d) larvae was observed. Note that the high proportion of 31- to 40-d-old larvae present in the southeasternmost region was actually captured just to the east of Browns Bank.

Calculations of the hatch dates of the larvae, based on their age and date of sampling, were used to identify and track discrete cohorts across cruises. However, high rates of apparent mortality reduced the number of cohort survivors to levels unsuited for monitoring the location of an individual cohort through time. As a proxy for true cohort tracking, the following analyses assume that the spatial distribution by age within a cruise resembles that of a single cohort through time.

Larval age should increase with distance from the spawning site if the larval drift hypothesis holds. The centre of abundance (centroid) for all but the oldest age category (excluding Georges Bank larvae) differed little among ages and cruises and showed relatively little displacement from Browns Bank. Centroid locations for the April (H133) and May (H135) cruises were closer to the northern cap of the bank than those depicted for the June (H137) cruise (Fig. 5). The position of the centroid corresponding to the oldest age category (age 65 d) in Fig. 5 is somewhat misleading in that it was based on a single capture. In a more sensitive test of the same larval drift corollary, the relationship between larval age and distance from Browns Bank was examined under the explicit assumption that the centre of Browns Bank was the spawning site. No relationship between distance and age was evident, either in terms of correlation or variance (Fig. 6). However, there was a suggestion of spatial clustering at all ages.

The results of the trend surface analysis were consistent with those above in demonstrating the presence of broadly dispersed spatial distributions within each age category. In fitting the model, spatial coordinate terms were nested within age for each cruise individually, since similarities in the distribution of larvae among ages and cruises could not be assumed. This model structure allowed linear, quadratic, and, in one case, cubic surfaces to be fit, although the higher order surfaces proved to be most informative (Table 2). The resulting model demonstrated that larval abundance differed significantly among most age categories (Table 3). Insufficient data were available for a significant fit to the April (H133) cruise data, while only one age category proved to be significant in the May (H135) cruise. In the June (H137) cruise, where larvae were most abundant, almost all model parameters were significant. Parameter significance in this context implies that spatial patterns in larval abundance were present. Note that the varying levels of station coverage among cruises (Table 1) only affect the precision of the parameter estimates and do not impair intercruise comparisons.

Contour plots of the fitted values from the trend surface models were used to examine the relative locations of each age category (Fig. 7). The spatial distributions of all age categories were centred on or around Browns Bank, although the centres appeared to shift to the northwest with age. A net northwestward movement of the larvae was also indicated by the orientation of the contour ellipses (with the exception of the 0- to 10-d-old larvae in June), while the flattening of the contour surface with age demonstrates increased dispersion with age.

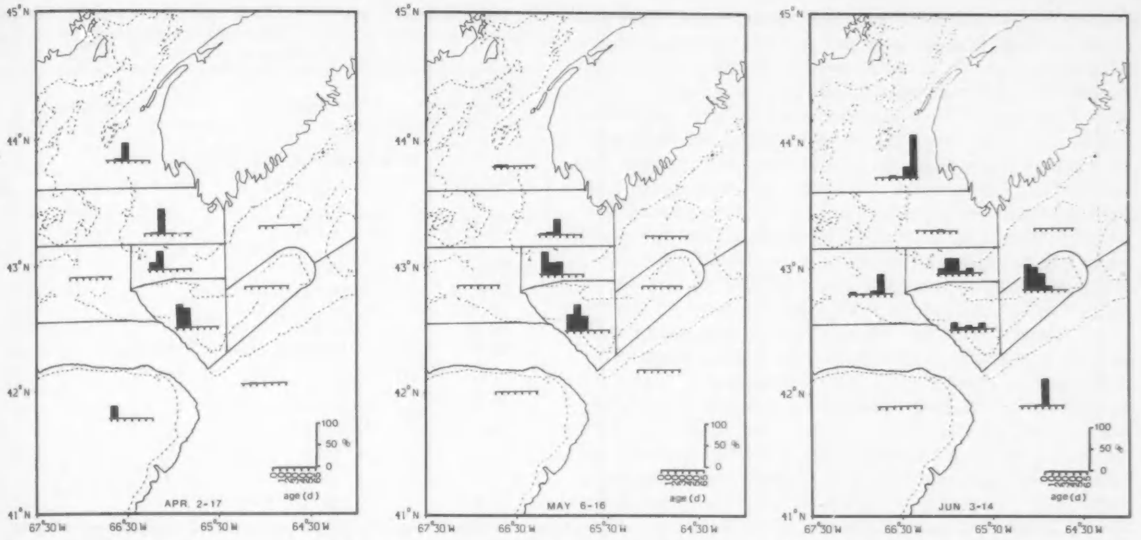

FIG. 4. Spatial distribution by age (days) of haddock larvae collected on each of three cruises in 1985. Histograms represent the proportion of each age category found within each region (regions delineated by heavy lines) relative to the total abundance of that age category within the cruise.

In the only age category successfully fitted with a cubic surface (age 11–20 d), an inshore–offshore bimodality in abundance was evident. The bimodality was not evident when a quadratic model was fitted to the same age–cruise data (Fig. 7). A comparison of the distributions of the 0- to 10-d-old larvae in May and June indicates a more easterly centre in the latter.

Discussion

This study clearly demonstrated that a significant proportion of the larval haddock were retained on or around Browns Bank. Larvae of all ages were consistently found in the vicinity of the bank. In addition, there was no significant shift in the centre of mass of the larvae with age, nor was there a significant relationship between age and distance from the Browns Bank spawning site. Since haddock do not spawn in southwestern Nova Scotia waters other than on Browns Bank (O'Boyle et al. 1984; Hurley and Campana 1989), the necessary corollaries of the retention hypothesis have been met. The presence of a tidally dominated circulation, resulting in a permanent gyre around the bank (Smith 1983, 1989; Loder et al. 1988), provides a physically based mechanism for the retention of the larvae. Yet with an egg stage duration of 12–19 d at ambient temperatures (Laurence and Rogers 1976), a mean water residence time of 14 d (Smith 1983, 1989), and a mean water displacement rate from the bank of 7.0 km/d (Campana et al. 1989), few of the older larvae should have been found anywhere near the bank. Indeed, both the trend surface analysis and the age-structured spatial distributions (Fig. 4) indicated that a significant proportion of the larvae were transported away from Browns Bank in a direction consistent both with the residual circulation and a previously postulated haddock drift model (Grosslein and Hennemuth 1973). While individual larvae cannot be both transported and retained, it appears that one part of the larval population was transported inshore from the spawning site, while the remainder was retained offshore longer than would be expected on the basis of water residence times.

In a parallel study of Browns Bank cod (Campana et al. 1989), a mechanism was suggested by which drift and retention processes might act in concert to split and disperse a larval population. The mechanism was based on the highly dispersive nature of the Browns Bank gyre. Individual particles in the gyre, such as drogues or ichthyoplankton, have the potential to exit the gyre very quickly or be retained for extended periods of time (Smith 1983, 1989; Loder et al. 1988). Of those larvae extruded from the gyre, many appeared to reside in what may be a region of reduced current flow between the bank and the 100-m contour (Campana et al. 1989; Hurley and Campana 1989). This area appears to be a shear zone between the Nova Scotia coastal current and the oppositely directed Browns Bank gyre. While there is, as yet, no physical basis for retention in this shear zone (Page and Smith 1989), high concentrations of larvae were consistently observed there. Irrespective of mechanism, displacement from this second region would almost certainly result in entrainment in the rapid flow of the coastal current, which proceeds in the same direction as that of the net movement of the larvae. The result of this three-stage process would be retention of some larvae on Browns Bank, retention of others in the region just north of the bank, and transport of others towards the inshore and/or mouth of the Bay of Fundy.

The results of the trend surface model provide strong support for the concept of a drift–retention dichotomy for individual haddock larvae. A dichotomy is clearly evident in the one age category successfully fitted with a cubic surface (Fig. 7: age 11–20 d); there, larvae are concentrated both on eastern Browns Bank and inshore along the 100-m bathymetric contour, but not in between. While a similar pattern would also be expected of the older larvae, such cannot be demonstrated with a quadratic surface. The quadratic representation of the cubic surface for age 11–20 d (Fig. 7) clearly shows the limitation of the quadratic model in highlighting a bimodal abundance contour. How-

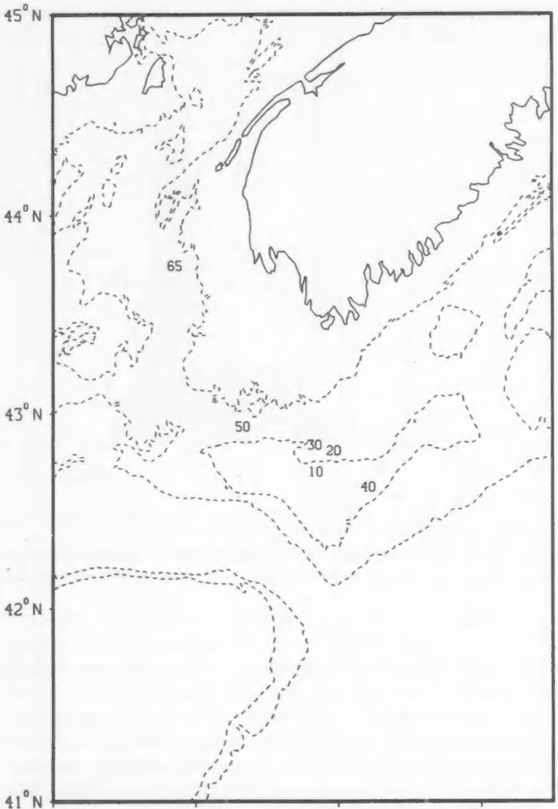

FIG. 5. Centres of abundance (centroids) for each of six age categories of larval haddock collected in June 1985. Age labels represent 0–10 (10), 11–20 (20), 21–30 (30), 31–40 (40), 41–50 (50), and 51–65 (65) d.

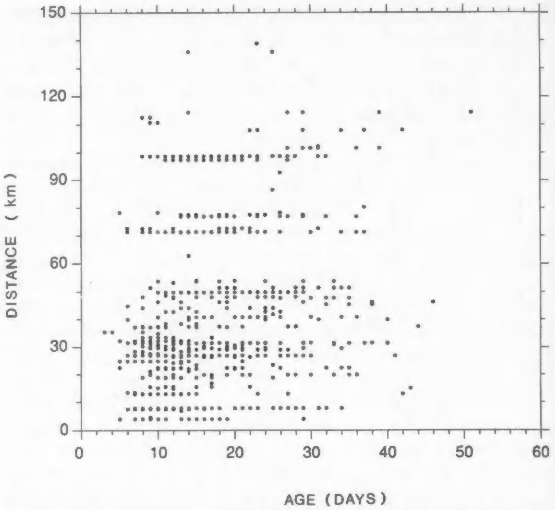

FIG. 6. Relationship between the age of larval haddock and their distance from the Browns Bank spawning site at the time of collection in June 1985.

TABLE 2. Analysis of deviance after fitting the trend surface model to the abundance of haddock larvae ((number/0.047)/m^2) according to age category and position of capture. P level refers to the χ^2 statistic.

Model	First difference in deviance	df	P level
	Cruise H135		
Mean + age	15.37	2	0.0000
Mean + age.linear	7.02	6	0.5355
Mean + age.quadratic	36.89	15	0.0000
	Cruise H137		
Mean + age	71.05	3	0.0000
Mean + age.linear	74.90	8	0.0000
Mean + age.quadratic	216.04	20	0.0000
Mean + age.cubic	247.56	36	0.0000

ever, in the same way that examination of residuals can be used to assess curvilinearity in a simple linear regression, maps of the residuals of the trend surface model can be used to reveal possible bimodal abundance patterns. On the basis of the residuals, the flat surfaces apparent in Fig. 7 for the older larvae appear to be the best quadratic approximation of a bimodal abundance contour, where larvae were concentrated both on eastern Browns Bank and inshore towards the mouth of the Bay of Fundy. Whether bimodality was present or not, the flat surfaces demonstrate that there was no spatial gradient in abundance within an age category; in other words, the older larvae were broadly distributed between the offshore and the inshore. This observation is most consistent with a dispersal process comprising both drift and retention components.

The drift–retention hypothesis appears to be robust to the assumptions and methodologies used in this study. The age determinations were probably accurate to within several days (Campana 1989), and the resulting larval age compositions were consistent both with expected mortality rates and observed spawning times (Hurley and Campana 1989). The five cruises spanned virtually all of the haddock spawning activity on Browns Bank (Hurley and Campana 1989) and appeared to circumscribe the larval distributions on all sides, although it is possible that the southeastern- and northern-most ranges of the older larvae were not surveyed. However, the presence of unsurveyed larvae in these regions would serve only to strengthen our conclusions. There was no evidence of drift from Georges Bank, either in this study or elsewhere (O'Boyle et al. 1984; Perry and Hurley 1986). While the use of bongo gear is known to be inappropriate for abundance estimation of older larvae and juveniles (Cushing 1986; Frank 1988; Suthers and Frank 1989), this study analyzed the relative spatial distribution within an age category, and thus was insensitive to any age-related gear avoidance that may have occurred.

Since trend surface models are new to fisheries applications, it is natural to question their value relative to more conventional approaches, such as the centroid and distance–age models used in Fig. 5 and 6. Trend surface models have been applied for years in geological, hydrological, and botanical contexts (Cliff and Ord 1981), where their utility for the interpretation of spatially structured data is now accepted. They are particularly valuable in the synthesis of multidimensional data; in the pre-

TABLE 3. Parameter estimates from Poisson trend surface models of haddock larval abundance ((number/0.047)/m^2). Ages 1–4 represent 0–10, 11–20, 21–30, and 31+ d, respectively.

Parameter	Estimate	Standard error
Cruise H135 (quadratic model)		
Mean	−1.97	0.93
Age 2 − Age 1	0.76	1.15
Age 3 − Age 1	−6.53	7.10
Age 1 terms		
Latitude	−12.98	6.04
Longitude	−15.63	6.44
Latitude^2	−26.78	11.01
Longitude^2	−24.54	11.04
Latitude × longitude	−44.31	19.90
Age 2 terms		
Latitude	−6.55	4.62
Longitude	−8.42	5.05
Latitude^2	−17.26	9.81
Longitude^2	−15.86	9.94
Latitude × longitude	−23.24	16.30
Age 3 terms		
Latitude	−5.55	18.75
Longitude	−34.96	43.83
Latitude^2	−6.25	14.73
Longitude^2	−51.79	69.38
Latitude × longitude	−21.00	57.37
Cruise H137 (quadratic model)		
Mean	−1.93	0.77
Age 2 − Age 1	3.10	0.80
Age 3 − Age 1	1.80	0.83
Age 4 − Age 1	0.31	0.96
Age 1 terms		
Latitude	−4.77	4.25
Longitude	1.36	1.77
Latitude^2	−12.45	9.69
Longitude^2	−0.42	2.24
Latitude × longitude	0.30	5.58
Age 2 terms		
Latitude	0.72	1.04
Longitude	2.58	0.69
Latitude^2	−16.46	3.66
Longitude^2	−2.55	1.02
Latitude × longitude	−7.89	2.37
Age 3 terms		
Latitude	1.84	1.15
Longitude	2.18	0.99
Latitude^2	−7.86	3.09
Longitude^2	−2.98	1.62
Latitude × longitude	−8.50	3.37
Age 4 terms		
Latitude	−0.64	1.56
Longitude	0.54	1.03
Latitude^2	−10.55	4.68
Longitude^2	−0.72	2.11
Latitude × longitude	−14.56	5.76
Cruise H137 (cubic model age 2 only)		
Mean	−1.74	0.88
Age 2 − Age 1	2.99	0.91
Age 2 terms		
Latitude	4.78	1.32
Longitude	3.92	0.77
Latitude^2	−23.19	6.05
Longitude^2	−2.05	1.33
Latitude × longitude	−8.27	3.63
Latitude^2 × longitude	−33.41	8.68
Latitude × longitude^2	−14.62	5.56
Latitude^3	−38.46	10.77
Longitude^3	−2.43	1.76

sent study, where larval abundance was a function of latitude, longitude, cruise, and age, conventional interpretation would have required the visual assimilation of 12 maps containing rather complex patterns of age-structured larval distribution and abundance. Further, interpretation would have been confounded by intercruise differences in survey coverage and station spacing. The trend surface approach was not subject to these constraints. The statistical structure of the trend surface model provided an objective basis for the resulting inferences about the spatial patterns. Deficiencies of the simpler centroid/distance–age models, such as the absence of directional information and confidence limits, and the inability to aggregate cruises, were not a factor in the trend surface model, making the latter not only more informative, but more reliable.

The trend surfaces associated with an analysis of Browns Bank cod (Campana et al. 1989) were not nearly as flat as those of haddock, indicating a more substantial drift component in the former. Since the two species of larvae were collected during the same cruises, a species-specific response to a single oceanographic system initially appears unlikely. There are three possible physical explanations. Firstly, the model formulation applied to cod differed from that applied to haddock: models were fitted on a cruise-by-cruise basis for haddock whereas cruises were treated as factors within a single model for cod. The latter formulation effectively smoothed out any cruise-to-cruise spatial pattern differences that might have existed for cod. Secondly, the cod and haddock may have had slightly different spawning locations on Browns Bank, and thus were affected to differing degrees by the retentive mechanism of the gyre. For instance, current speeds appear to be lower on the eastern half of the bank than on the western half (Loder and Greenberg 1986). However, if differences in spawning location did exist, they were on a scale that could not be resolved (Hurley and Campana 1989). Finally, and we consider this to be the most likely explanation, the balance between drift and retention for cod and haddock may have differed because of differences in spawning dates in conjunction with short-term changes in gyre stability. Changes in gyre stability may occur over a much shorter time scale (Smith 1989) than the interval between peak larval abundances of cod (April–May) and haddock (June) and thus result in an apparently species-specific response. Support for the concept of timing effects comes from the nearly identical trend surfaces for cod and haddock of ages 0–10 d in the May cruise, the only cruise and age where both species were adequately represented. The influence of short-term changes in gyre stability is best demonstrated by a comparison of the distribution of the youngest haddock larvae between the May and June cruises; a substantial shift in distribution is apparent between the two cruises. All of the above suggests that seasonal timing, more than interspecific differences, is influential in affecting the relative balance between drifted and retained larvae.

There is no evidence to suggest that behaviour aided in the retention of larval haddock around Browns Bank. While larval retention has often been linked to vertical migration patterns (Fortier and Leggett 1983; Sinclair and Iles 1988), the latter was not evident in a study of Browns Bank haddock larvae (unpublished observations). Physically based drift and retention mechanisms must clearly be invoked to explain the observed distribution of nonmotile eggs and young larvae, but similar arguments may not apply to the older larvae. Since few larvae greater than 40 d old (corresponding to a length of approximately 7 mm (Campana and Hurley 1989) were captured, sev-

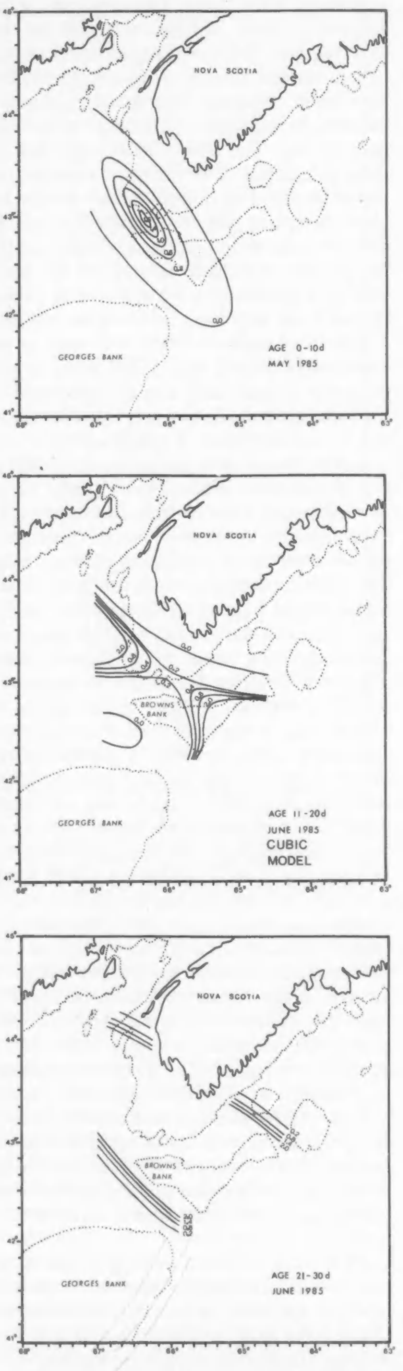
NOVA SCOTIA
GEORGES BANK
BROWNS BANK
AGE 0-10d
MAY 1985
AGE 0-10d
JUNE 1985
AGE 11-20d
JUNE 1985
CUBIC
MODEL
AGE 11-20d
JUNE 1985
QUADRATIC
MODEL
AGE 21-30d
JUNE 1985
AGE 31+d
JUNE 1985
0.0
0.2
0.4
0.6
0.8
1.4
2.0
45°
44°
43°
42°
41°
68°
67°
66°
65°
64°
63°

FIG. 7. Contours of haddock larval abundance ((numbers/0.047)/m^2) in May and June of 1985 for each of four daily age categories. Contours represent results of fitted quadratic trend surface models, with the exception of ages 11–20 d which were also fitted with a cubic surface. Abundances are in units of 10^{-3} for ages 21–30 and 31+ d.

eral months of life history were unsampled prior to settling (Koeller et al. 1986). A distribution of settled juveniles (Grosslein and Hennemuth 1973) similar to that of larvae greater than 20 d old is consistent with the concept of enhanced retention in older larvae.

Proponents of both the larval drift (Cushing 1986) and retention (Sinclair 1988) hypotheses now agree that the two concepts are not necessarily mutually exclusive. While the possibility of drift within a retention zone has been acknowledged, the segregation of a single population by both drift and retention proceses is, to our knowledge, unique. In an elaboration of the retention hypothesis (the member–vagrant hypothesis), emphasis was placed upon population discreteness during the early life history stage rather than larval fidelity to the spawning site (Sinclair 1988; Sinclair and Iles 1988). Under these conditions, the entire region between Browns Bank and the inshore would have to be considered a single retention zone. The alternative interpretation would be that all larvae that exit the bank are "vagrants" and thus lost to the population gene pool. Given the continuous band of settled young-of-the-year stretching from Browns Bank to the mouth of the Bay of Fundy (Grosslein and Hennemuth 1973) and the significant portion of the stock found off-bank (Bowen 1987), the vagrancy interpretation appears unlikely.

Whether placed in the context of the member–vagrant hypothesis or not, a drift–retention dichotomy has significant implications for both recruitment and stock structure studies of Browns Bank haddock. Segregation of the population into inshore and offshore components would appear to maximize the probability of population survival in the face of adverse (and spatially variable) conditions. A prerequisite of this adaptive strategy would be that survival/environmental conditions differ between the inshore and offshore. Since the relative contribution of the drifted/retained larvae to a given cohort would depend on the "leakiness" of the Browns Bank gyre, overall cohort survival may vary with gyre activity. As noted previously, changes in gyre stability may occur on a very short time scale. While the cod–haddock comparison assumed interspecific similarities in behaviour and vertical distribution, it supported the idea that intraannual variations in gyre stability may be important in determining the balance between drift and retention. Such variations, integrated over a spawning season, might then help explain year-to-year variations in year-class strength. A test of this hypothesis would require a quantitative index of gyre leakiness that could then be related to independent indices of year-class strength. Intraannual gyre variations, in conjunction with species-specific spawning times, may also explain apparent asynchronies in year-class strengths between Browns Bank cod and haddock. Speculations aside, the drift–retention dichotomy on Browns Bank highlights the potential flexibility in larval dispersal strategies and suggests that undescribed permutations of the drift–retention continuum may yet exist in other systems.

Acknowledgements

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References

BOWEN, W. D. 1987. A review of stock structure in the Gulf of Maine area: a workshop report. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 87/21: 51 p.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER. 1976. Daily growth increments in otoliths from larval and adult fishes. Fish Bull. 74: 1–8.

CAMPANA, S. E. 1989. Otolith microstructure of three larval gadids in the Gulf of Maine, with inferences on early life history. Can. J. Zool. 67: 1401–1410.

CAMPANA, S. E., AND P. C. F. HURLEY. 1989. An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 46: 603–613.

CAMPANA, S. E., AND J. D. NEILSON. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42: 1014–1032.

CAMPANA, S. E., S. J. SMITH, AND P. C. F. HURLEY. 1989. An age-structured index of cod larval drift and retention in the waters off of Southwest Nova Scotia. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 191: 50–62.

CLIFF, A. D., AND J. K. ORD. 1981. Spatial processes. Models and applications. Pion Limited, London.

CUSHING, D. H. 1972. The production cycle and the numbers of marine fish. Symp. Zool. Soc. Lond. 29: 213–232.

1986. The migration of larval and juvenile fish from spawning ground to nursery ground. J. Cons. Int. Explor. Mer 43: 43–49.

ELLERTSEN, B., P. FOSSUM, P. SOLEMDAL, S. SUNDBY, AND S. TILSETH. 1984. A case study on the distribution of cod larvae and availability of prey organisms in relation to physical processes in Lofoten, p. 453–477. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod (*Gadus morhua* L.). Flodevigen Rapportser 1.

FORTIER, L., AND W. C. LEGGETT. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Can. J. Fish. Aquat. Sci. 40: 1543–1555.

FRANK, K. T. 1988. Independent distributions of fish larvae and their prey: natural paradox or sampling artifact? Can. J. Fish. Aquat. Sci. 45: 48–59.

GAGNÉ, J. A., and R. N. O'Boyle. 1984. The timing of cod spawning on the Scotian Shelf, p. 501–517. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod (*Gadus morhua* L). Flodevigen Rapportser 1.

GROSSLEIN, M. D., AND R. C. HENNEMUTH. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 77–88.

HARDEN-JONES, F. R. 1968. Fish migration. Edward Arnold Ltd., London. 325 p.

HURLEY, P. C. F., AND S. E. CAMPANA. 1989. Distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in the waters off Southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46: (This issue).

ILES, T. D., AND M. SINCLAIR. 1982. Atlantic herring: stock discreteness and abundance. Science (Wash., DC.) 215: 627–633.

JAHN, A. E., AND R. J. LAVENBERG. 1986. Fine-scale distribution of nearshore, suprabenthic fish larvae. Mar. Ecol. Prog. Ser. 31: 223–231.

KENDALL, A. W., JR., M. E. CLARKE, M. M. YOKLAVICH, AND G. W. BOEHLERT. 1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 85: 499–521.

KOELLER, P. A., P. C. F. HURLEY, P. PERLEY, AND J. D. NEILSON. 1986. Juvenile fish surveys on the Scotian Shelf: implications for year-class size assessments. J. Cons. Int. Explor. Mer 43: 59–76.

LAURENCE, G. C., AND C. A. ROGERS. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus*). J. Cons. Int. Explor. Mer 36: 220–228.

LEAR, W. H., AND J. M. GREEN. 1982. Migrations of the 'northern' Atlantic cod and the mechanisms involved, p. 309–215. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill. [ed.] Mechanisms of migration in fishes. Plenum Press, New York, NY.

LOCKWOOD, S. J., AND W. LUCASSEN. 1984. The recruitment of juvenile plaice (*Pleuronectes platessa* L.) to their parent spawning stock. J. Cons. Int. Explor. Mer 41: 268–275.

LODER, J. W., AND D. A. GREENBERG. 1986. Predicted positions of tidal fronts in the Gulf of Maine region. Cont. Shelf Res. 6: 397–414.

LODER, J. W., C. K. ROSS, AND P. C. SMITH. 1988. A space and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. 45: 1860–1885.

McCleave, J. D., J. J. M. Bedeaux, P. G. Doucet, J. C. Jager, J. T. L. Jong, W. J. Van der Steen, and B. Voorzanger. 1987. Statistical methods for analysis of plankton and nekton distribution, with application to selective tidal stream transport of juvenile American eels (*Anguilla rostrata*). J. Cons. Int. Explor. Mer 44: 90–103.

McCullagh, P., and J. A. Nelder. 1983. Generalized linear models. Chapman and Hall, London. 261 p.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 183: 27–40.

Ouellet, P., and J. J. Dodson. 1985. Tidal exchange of anadromous rainbow smelt (*Osmerus mordax*) larvae between a shallow spawning tributary and the St. Lawrence estuary. Can. J. Fish. Aquat. Sci. 42: 1352–1358.

Page, F. H., and P. C. Smith. 1989. Particle dispersion in the surface layer off southwest Nova Scotia: description and evaluation of a model. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): (This issue).

Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., DC) 173: 1124–1127.

Payne, C. D. [ed.] 1986. The GLIM (Generalized Linear Interactive Modelling) system manual. Numerical Algorithms Group, Oxford.

Perry, R. I., and P. C. F. Hurley. 1986. Circulation and potential ichthyoplankton dispersal in the Gulf of Maine, Browns and Georges Bank areas. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 86/37: 16 p.

Power, J. H. 1986. A model of the drift of northern anchovy, *Engraulis mordax*, larvae in the California Current. Fish. Bull. 84: 585.

Ripley, B. D. 1982. Spatial statistics. John Wiley & Sons, New York, NY.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle, WA. 252 p.

Sinclair, M., and T. D. Iles. 1988. Population richness of marine fish species. Aquat. Living Resour. 1: 71–83.

Smith, P. C. 1983. The mean and seasonal circulation off southwest Nova Scotia. J. Phys. Oceanogr. 13: 1034–1054.

1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

Smith, W. G., and W. W. Morse. 1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. Mar. Ecol. Prog. Ser. 24: 1–13.

Suthers, I. M., and K. T. Frank. 1989. Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in Southwestern Nova Scotia determined with two different gear types. Can. J. Fish. Aquat. Sci. 46: 591–602.

Distribution and Abundance of Haddock (*Melanogrammus aeglefinus*) and Atlantic Cod (*Gadus morhua*) Eggs and Larvae in the Waters off Southwest Nova Scotia[1]

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Hurley, P. C. F., and S. E. Campana. 1989. Distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in the waters off southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 103–112.

Synoptic ichthyoplankton surveys conducted at monthly intervals during the winter–spring of 1983–85 were used to determine the location, timing, and magnitude of spawning by haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) off southwest Nova Scotia. There was a marked similarity in the spawning locations of the two species: primary spawning occurred on Browns Bank, although lower levels of spawning were observed on adjacent banks and in the inshore region. Cod egg abundance peaked in April in all years, while that of haddock varied between April–June.

À l'hiver et au printemps de 1983 à 1985, des relevés synoptiques de l'ichtyoplancton ont été faits à intervalles mensuels afin de déterminer l'emplacement, le moment et l'importance de la fraie de l'aiglefin (*Melanogrammus aeglefinus*) et de la morue franche (*Gadus morhua*) au large de la rive sud-ouest de la Nouvelle-Écosse. On a observé une similarité marquée des emplacements choisis par les deux espèces : la fraie primaire a eu lieu sur le banc Browns, bien qu'une fraie moins importante ait été observée sur les bancs adjacents et vers la côte. Les oeufs de morue étaient les plus abondants au mois d'avril de chaque année alors que dans le cas de l'aiglefin, l'abondance maximale variait entre avril et juin.

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While many workers have reported spawning activity of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) off Southwest Nova Scotia, none of the studies have been conducted in sufficient spatial or temporal detail to clearly delineate the spawning season or location. Previous work has shown that spawning of both species may occur anywhere between January and June, with peak spawning in April and May for cod and haddock, respectively (Bigelow and Schroeder 1953; Homans and Vladykov 1954; Serebryakov 1971; Grosslein and Hennemuth 1973; Scott 1983; Gagné and O'Boyle 1984; O'Boyle et al. 1984; Markle and Frost 1985; Koslow et al. 1985; Smith and Morse 1985; Sherman et al. 1987). The centre of spawning has generally been acknowledged to be Browns Bank, with lesser centres on adjacent banks.

An objective of the present study was to determine the timing and location of spawning of haddock and Atlantic cod off Southwest Nova Scotia, by examining the distribution and abundance of their eggs and larvae. A second objective was to assess the intraseasonal, interannual, and spatial variability in location, timing, and magnitude of spawning of these species.

Materials and Methods

A grid of 95 stations off Southwest Nova Scotia was sampled once a month from February to June during 1983 to 1985. Stations were spaced approximately 28 km apart, with additional stations in the vicinity of Browns Bank (Fig. 1). Two extra transects across Browns Bank were added to the grid in 1984 and 1985. Cruise dates and number of stations sampled are shown in Table 1.

At each station, an oblique tow was made with a paired 61-cm diameter bongo sampler, to a depth of 5 m off bottom or to a maximum depth of 200 m. Sampler depth was determined from a Guildline conductivity–temperature–depth (CTD) sensor attached just above the sampler. The bongo frame was fitted with 333-μm mesh Nitex nets and volume filtered was determined from calibrated General Oceanics flowmeters centred in the mouth of each net. Vessel speed was maintained at 2.5 knots (1.3 m/s) and wire rates in and out were 50 and 20 m/min, respectively. During 1984 and 1985, tows at each station were replicated immediately, using the same starting location and vessel heading. Samples were fixed in 5% buffered formalin in seawater. Marble chips were used as a buffer during 1983. In 1984 and 1985, sodium carbonate was used as a buffer and samples were transferred to 95% ethanol after 48 h.

Fish eggs and larvae were removed and identified from the preserved samples in the laboratory. Samples containing more than 200 eggs were subsampled using the beaker split method (Van Guelpen et al. 1982) to obtain a subsample containing between 100 and 200 eggs. Eggs were classified into the following four developmental stages (after Markle and Frost 1985): Stage I, from spawning until the visible formation of an embryonic axis about the midgastrula; Stage II, from the end of Stage

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[1] Fisheries Ecology Program Contribution Number : 14.

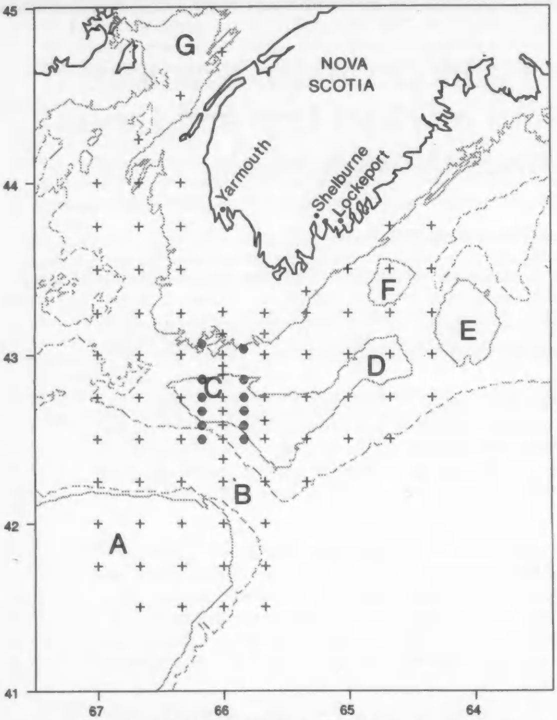

FIG. 1. Map of study area showing station locations and geographic features referred to in the text: (A) Georges Bank; (B) Fundian Channel; (C) Browns Bank; (D) Baccaro Bank; (E) La Have Bank; (F) Roseway Bank; and (G) Bay of Fundy. Stations added in 1984 and 1985 are indicated by circles (⊕). Contours are 100- and 200-m isobaths.

TABLE 1. Summary of cruise dates and number of stations sampled during this study.

Cruise	Start date	End date	N
H091	83-02-09	83-02-17	53
H093	83-03-06	83-03-16	50
P288	83-04-07	83-04-20	49
H097	83-05-04	83-05-13	78
H099	83-06-04	83-06-12	81
H112	84-02-08	84-02-15	74
H114	84-03-22	84-03-29	53
H116	84-04-17	84-04-25	62
H118	84-05-15	84-05-23	70
H120	84-06-12	84-06-21	83
H130	85-02-05	85-02-21	85
H132	85-03-14	85-03-27	48
H133	85-04-03	85-04-17	92
H135	85-05-07	85-05-14	57
H137	85-06-04	85-06-13	61

I until the embryo is half way around the yolk, approximately the time of blastopore closure; Stage III, from the end of Stage II until the tip of the tail reaches or could reach the snout; and Stage IV, from the end of Stage III until hatching. Early egg stages of cod, haddock and witch flounder (*Glyptocephalus cynoglossus*) could not be differentiated, and thus were artificially grouped as CHW (cod, haddock, witch). These species could only be identified after late Stage III, when diagnostic pigmentation had formed. Standard length of larvae (less than 18 mm) was measured to the nearest millimetre.

Sample abundance was calculated as the number per square metre using maximum tow depth; station abundance was calculated as the mean of all samples available for each station.

Results

Stage I CHW eggs off Southwest Nova Scotia were taken in all cruises, primarily on Browns Bank, but lower levels were encountered throughout the area, including the inshore (Fig. 2). Since Stage I eggs are less than 7 d old (Marak and Colton 1961; Fridgeirsson 1978; Page and Frank 1989), their distribution should provide a more accurate indication of spawning location than that of Stage IV. This assumes that the relative contribution of witch eggs is low, an assumption that is supported by studies showing that Stage IV witch eggs were largely absent from the Scotian Shelf prior to May (Markle and Frost 1985; Neilson et al. 1988). We found no Stage IV witch eggs prior to June in each of the 3 yr, with the exception of one station each in May 1984 and 1985.

The temporal distribution of Stage IV haddock eggs was more variable than that of cod (Figs. 3 and 4). During 1983, haddock eggs were not observed off Southwest Nova Scotia until April, in contrast to their first appearance in March 1984 and February 1985. Cod eggs were present in February in all 3 yr. Peak haddock egg abundance was observed in April, May, and June of 1983, 1985, and 1984, respectively, but substantial numbers were evident in June of all 3 yr. Peak cod egg abundance was observed in April of all 3 yr.

Haddock larvae off Southwest Nova Scotia appeared 1 mo after eggs were first observed, while cod larvae were observed in all cruises (Figs. 5 and 6). Only 10 haddock larvae were taken off Southwest Nova Scotia in 1983, while 450 were taken in 1984 (almost all in June) and 1335 in 1985 (in April, May, and June) (Table 2). Cod larvae (Table 3) were infrequently captured in 1983 and 1984 (total of 15 and 27, respectively), some of which hatched from eggs spawned the previous November, December, and January (Campana and Hurley 1989). The abundance of larval cod was highest in 1985, with a total of 408 larvae taken.

Maximum egg and larval station abundances of both cod and haddock were generally higher on Georges Bank than on Browns Bank (Figs. 3, 4, 5 and 6). Although coverage of stations on Georges Bank was sporadic, eggs of both species tended to appear 1 to 2 mo earlier there than off Southwest Nova Scotia.

Discussion

Our study confirms earlier reports that Browns Bank is the principle spawning ground of both cod and haddock in Southwest Nova Scotia (Scott 1983; Gagné and O'Boyle 1984; O'Boyle et al. 1984; Koslow et al. 1985; Waiwood and Buzeta 1989). Lower levels of spawning were observed on Baccaro, Roseway, and La Have banks for both species. The marked similarity between cod and haddock ichthyoplankton distributions implies that the two species utilize the same spawning sites, and that the same physical forces may be influencing the subsequent distribution of their eggs and larvae (Campana et al. 1989a,b). Repeated observations of Stage I eggs in the nearshore region are most consistent with inshore spawning, since

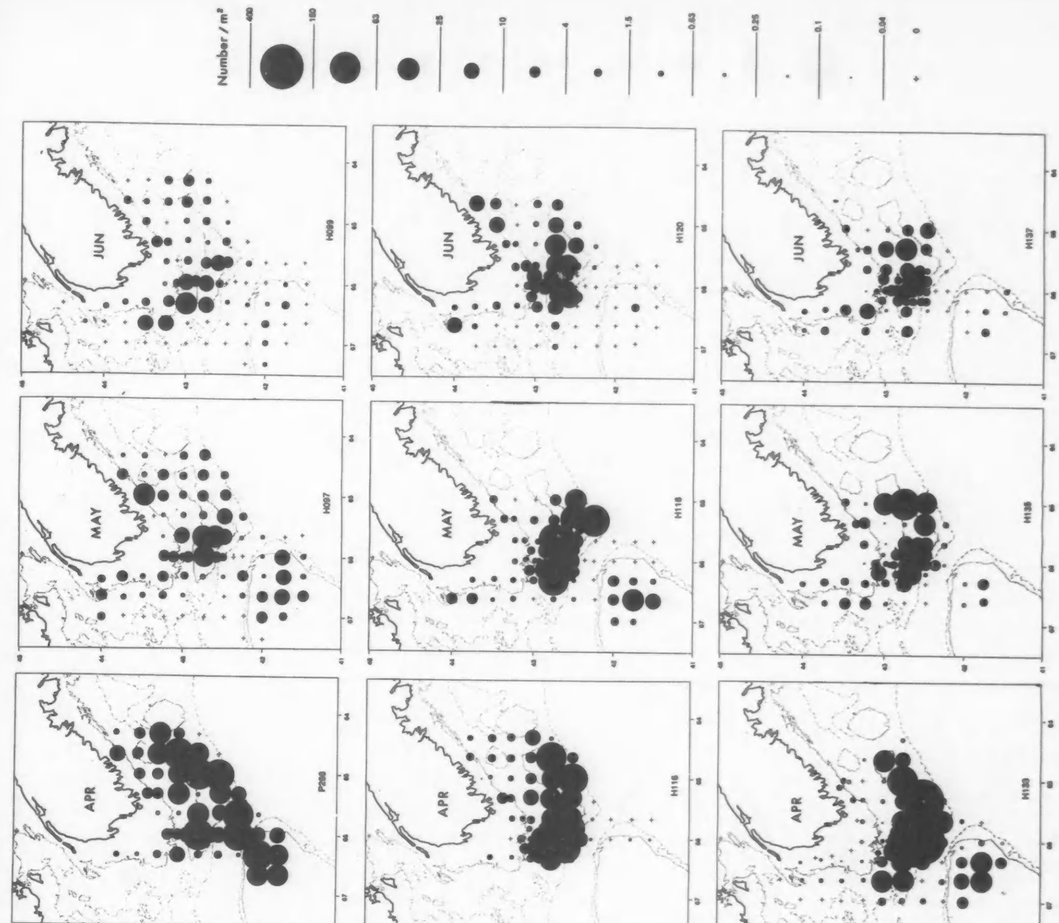
Number / m²
400
160
63
25
10
4
1.5
0.63
0.25
0.1
0.04
0
1983
FEB
H091
MAR
H093
APR
P266
MAY
H097
JUN
H099
1984
FEB
H112
MAR
H114
APR
H116
MAY
H118
JUN
H120
1985
FEB
H130
MAR
H132
APR
H133
MAY
H135
JUN
H137

FIG. 2. Distribution of Stage I CHW (cod/haddock/witch) eggs by month and year, 1983–85 (number/m²).

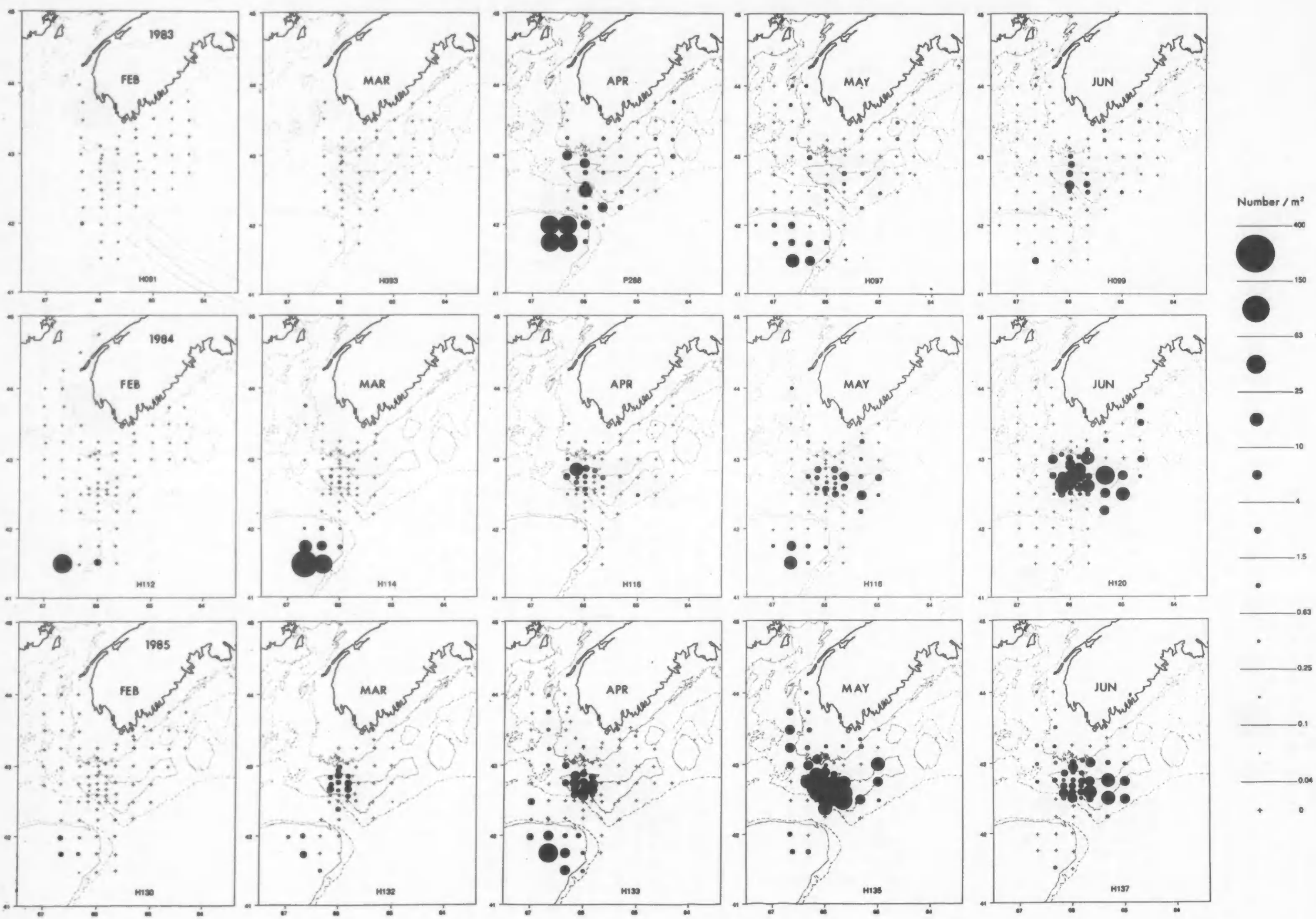
1983
FEB
H091
MAR
H093
APR
P288
MAY
H097
JUN
H099
1984
FEB
H112
MAR
H114
APR
H116
MAY
H118
JUN
H120
1985
FEB
H130
MAR
H132
APR
H133
MAY
H135
JUN
H137
Number / m²
400
150
63
25
10
4
1.5
0.63
0.25
0.1
0.04
0

FIG. 3. Distribution of Stage IV haddock eggs by month and year, 1983–85 (number/m^2).

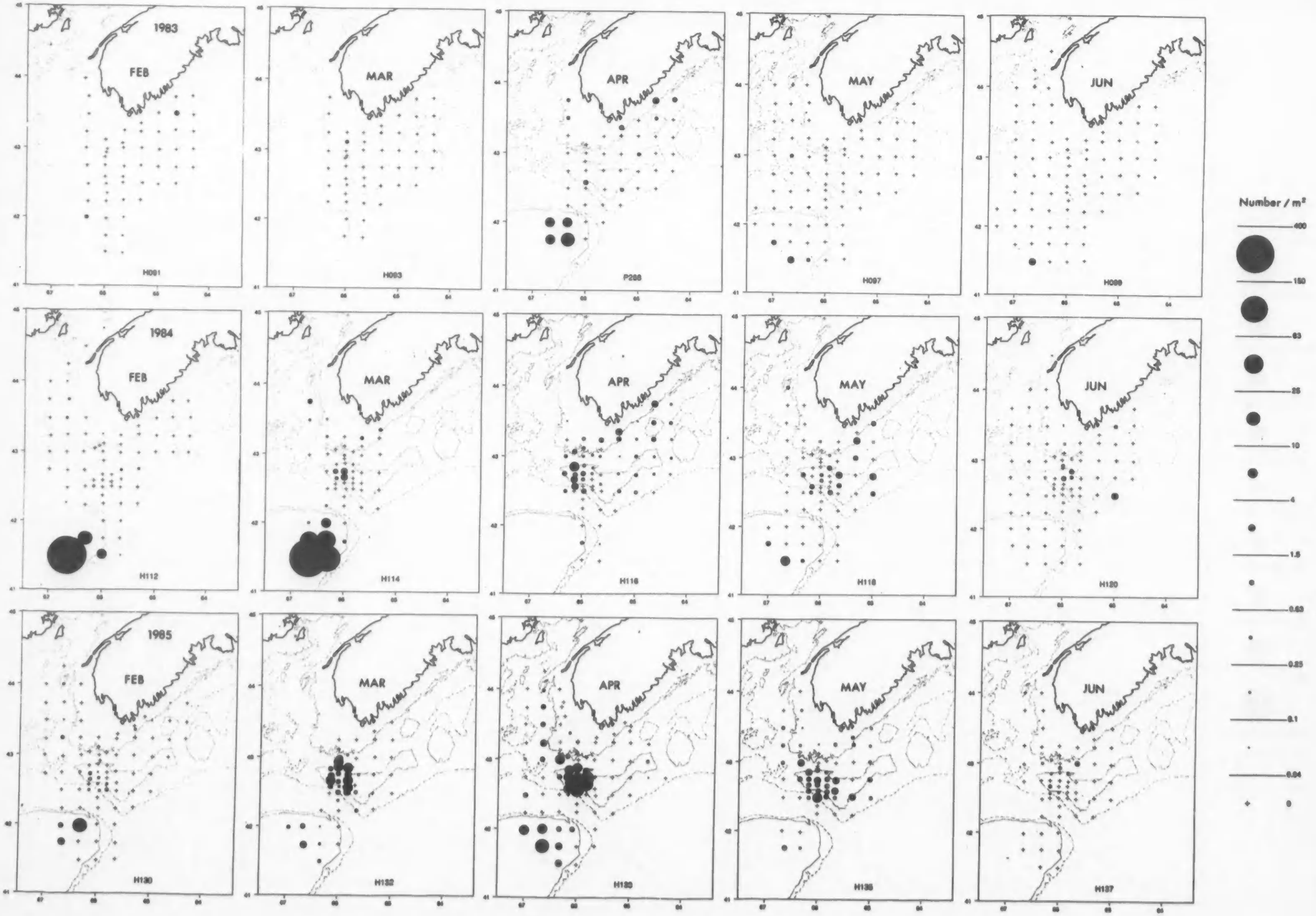
1983
FEB
MAR
APR
MAY
JUN
H081
H083
P288
H097
H099
1984
FEB
MAR
APR
MAY
JUN
H112
H114
H116
H118
H120
1985
FEB
MAR
APR
MAY
JUN
H130
H132
H133
H135
H137
45
44
43
42
41
67
66
65
64
Number / m²
400
150
63
25
10
4
1.5
0.63
0.25
0.1
0.04
0

FIG. 4. Distribution of Stage IV cod eggs by month and year, 1983–85 (number/m²).

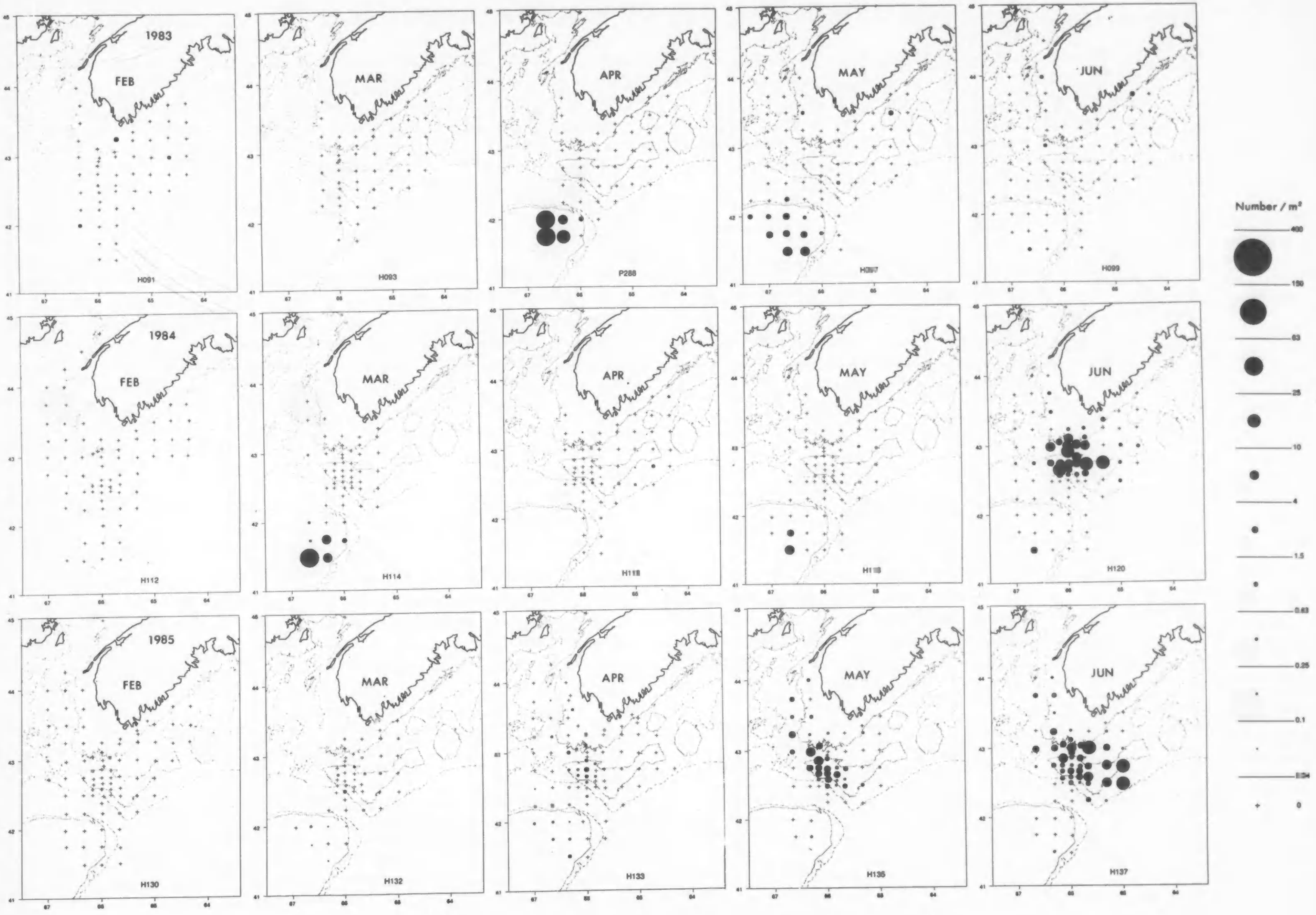
1983
FEB
H091
MAR
H093
APR
P288
MAY
JUN
H099
1984
FEB
H112
MAR
H114
APR
MAY
JUN
H120
1985
FEB
H130
MAR
H132
APR
H133
MAY
H135
JUN
H137
45
44
43
42
41
67
66
65
64
Number / m²
400
150
63
25
10
4
1.5
0.63
0.25
0.1
0.04
0

FIG. 5. Distribution of haddock larvae by month and year, 1983–85 (number/m²).

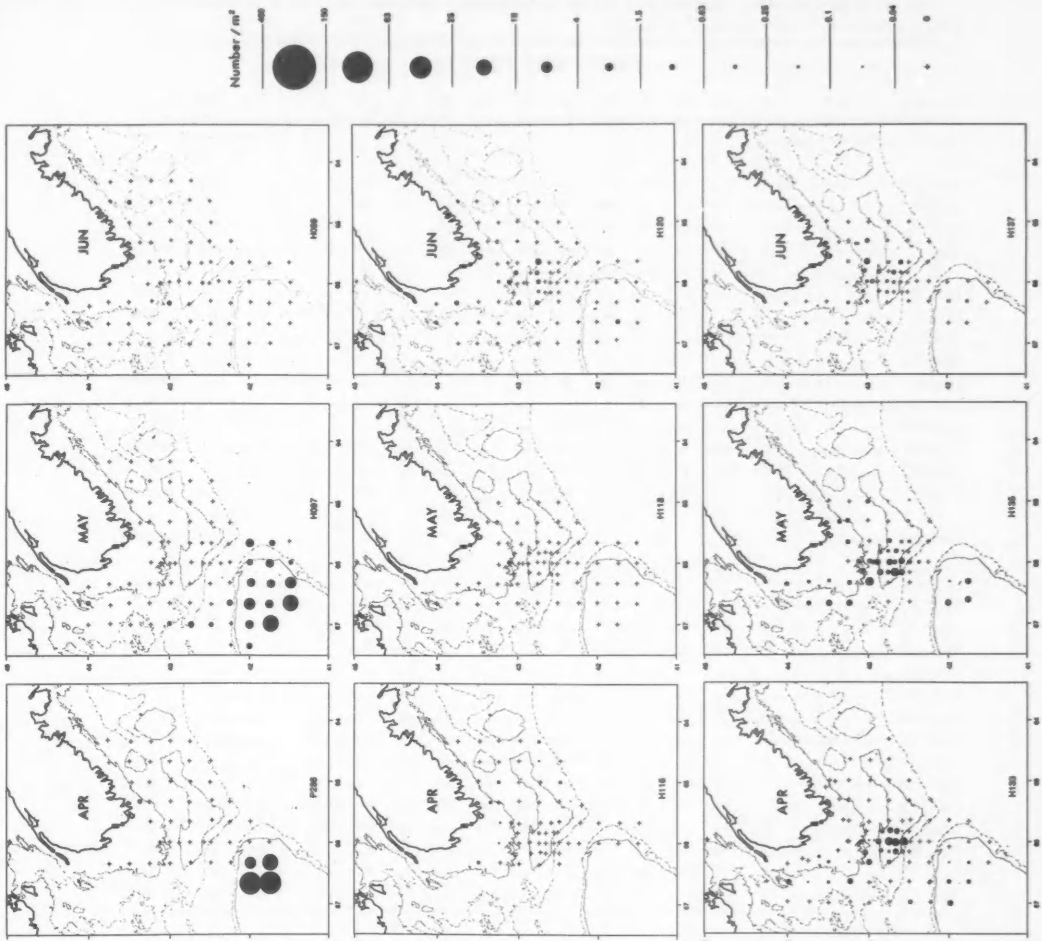
Number / m²
160
63
25
4
1.5
0.63
0.25
0.1
0.04
0
1983
FEB
H091
MAR
H093
APR
P286
MAY
H097
JUN
H098
1984
FEB
H112
MAR
H114
APR
H116
MAY
H118
JUN
H120
1985
FEB
H130
MAR
H132
APR
H133
MAY
H136
JUN
H137

FIG. 6. Distribution of cod larvae by month and year, 1983–85 (number/m²).

TABLE 2. Length frequency (numbers) of haddock larvae taken off Southwest Nova Scotia and on Georges Bank, by month and year 1983–85.

	Standard length (mm)																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
Southwest Nova Scotia																		
Feb. 83	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	2
Mar. 83	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Apr. 83	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
May 83	—	1	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	4
Jun. 83	—	—	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	4
Feb. 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mar. 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Apr. 84	—	—	1	5	2	1	2	—	1	—	—	—	—	—	—	—	—	12
May 84	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	2
Jun. 84	—	1	25	187	136	50	26	9	—	2	—	—	—	—	—	—	—	436
Feb. 85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mar. 85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Apr. 85	—	—	23	20	1	—	—	—	—	—	—	—	—	1	—	—	—	45
May 85	—	44	217	67	11	6	1	—	—	—	—	—	—	—	—	—	—	346
Jun. 85	—	49	272	236	195	114	64	9	3	1	—	—	—	—	1	—	—	944
Georges Bank																		
Feb. 83	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Mar. 83	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Apr. 83	—	4	59	83	18	12	5	2	—	—	—	—	—	—	1	—	—	184
May 83	—	—	8	21	11	3	5	3	2	4	4	6	5	5	2	2	2	83
Jun. 83	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Feb. 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mar. 84	—	5	65	108	40	3	—	—	—	—	—	—	—	—	—	—	—	221
Apr. 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
May 84	—	—	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	6
Jun. 84	—	—	—	4	—	2	—	—	—	—	—	—	—	—	—	—	—	6
Feb. 85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mar. 85	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	4
Apr. 85	—	1	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	8
May 85	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Jun. 85	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1

reported current speeds (Lawrence and Trites 1983; Smith 1983, 1989) are of insufficient magnitude to have carried the eggs from Browns Bank during the 6-d (maximum) stage duration (Marak and Colton 1961; Page and Frank 1989). However, the magnitude of inshore spawning appeared to be low relative to the total. While inshore spawning of cod has been reported previously (Bigelow and Schroeder 1953; Gagné and O'Boyle 1984; O'Boyle et al. 1984), the inshore distribution of Stage IV haddock eggs suggests that haddock may also spawn inshore. Note that earlier reports of apparent inshore haddock spawning (McKenzie 1940; Kohler 1960) were based on inconclusive data.

There was a marked consistency among the apparent spawning sites for both cod and haddock. Aside from differences in relative abundance, the stage IV eggs of both species were characterized by similar distributions, despite differences in spawning times and associated circulation pattern changes. There was little or no evidence of interannual shifts in spawning location. If, as Waiwood and Buzeta (1989) have suggested, spawning location of haddock is linked to sediment type, this may explain the observed interannual consistency. An equally viable explanation is the correspondence between spawning sites and bottom topography, which is itself correlated with sediment type. Apparent geographic shifts in spawning location, from west to east, within a spawning season, were consistent across years, and were probably linked to patterns in vernal warming (Drinkwater and Trites 1987). A similar trend in flatfish spawning on the Scotian Shelf was reported by Neilson et al. (1988). Reexamination of the cod egg data presented by Gagné and O'Boyle (1984) suggests that the same may apply to cod along the entire Scotian Shelf.

The time of peak spawning for cod (April) and haddock (April–June) off Southwest Nova Scotia is similar to that reported elsewhere for eastern Scotian Shelf stocks (Gagné and O'Boyle 1984; O'Boyle et al. 1984). It is also consistent with estimates of peak spawning activity derived from observations of spawning fish (Scott 1983) and examination of otolith microstructure (Campana 1989). However, our data indicate that haddock spawning is more prolonged than was previously described. Further, the timing of peak spawning varied among years, occurring in each of the months April through June. The source of these interannual differences is not immediately evident, nor were similar variations observed in relation to cod spawning. Cod spawning was usually initiated earlier than that of haddock, but the lag between their peak times was not always of the same duration (0–2 mo). While this study was not designed to examine any contribution by fall spawners (Gagné and O'Boyle 1984), some fall progeny were evident among the

TABLE 3. Length frequency (numbers) of cod larvae taken off Southwest Nova Scotia and on Georges Bank, by month and year 1983–85.

	Standard length (mm)																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
Southwest Nova Scotia																		
Feb. 83	—	—	—	1	1	—	1	—	—	—	—	—	—	—	1	—	1	5
Mar. 83	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	2
Apr. 83	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
May 83	—	—	—	—	1	—	—	—	—	—	—	—	1	1	1	—	1	5
Jun. 83	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	2
Feb. 84	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
Mar. 84	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Apr. 84	—	—	1	2	1	2	2	—	—	—	—	—	—	—	—	2	—	10
May 84	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Jun. 84	—	1	—	4	6	2	—	—	—	—	—	1	—	—	—	—	—	14
Feb. 85	—	1	2	3	1	2	—	2	—	—	1	—	—	—	—	—	1	13
Mar. 85	—	—	4	21	6	—	—	—	—	—	1	—	—	—	—	—	—	32
Apr. 85	—	4	59	89	21	5	—	1	—	—	—	—	—	—	—	—	1	180
May 85	—	5	38	41	34	13	8	5	—	2	1	—	—	1	1	—	—	149
Jun. 85	—	2	7	8	1	3	2	3	1	—	4	—	—	—	—	2	1	34
Georges Bank																		
Feb. 83	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1
Mar. 83	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Apr. 83	—	—	13	51	34	36	40	25	11	5	2	2	1	—	—	—	—	220
May 83	—	—	—	—	—	3	2	6	3	14	8	11	18	23	28	13	16	145
Jun. 83	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Feb. 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mar. 84	—	13	79	196	95	16	4	—	—	1	—	—	—	—	—	—	—	404
Apr. 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
May 84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Jun. 84	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
Feb. 85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
Mar. 85	—	—	3	9	1	—	—	—	—	—	—	—	—	—	—	—	—	13
Apr. 85	—	5	8	2	2	—	—	—	—	—	—	—	—	—	—	—	—	17
May 85	—	—	—	—	1	—	—	—	—	1	—	2	3	6	2	2	3	20
Jun. 85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0

larvae collected in this study. Peak spawning on Georges Bank occurred 1–2 mo earlier than on Browns Bank for both species, in keeping with other published findings (Grosslein and Hennemuth 1973; Colton et al. 1979; Sherman et al. 1987).

Interannual and interspecific comparisons of egg and larval production are beyond the scope of this paper, and in any case, have been addressed elsewhere (Campana et al. 1989c). However, on the basis of visual inspection of the data, there appears to be little evidence of either synchrony in relative abundance or exchange of ichthyoplankton between Browns and Georges banks (Smith and Morse 1985; Perry and Hurley 1986).

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References

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

CAMPANA, S. E. 1989. Otolith microstructure of three larval gadids in the Gulf of Maine, with inferences on early life history. Can. J. Zool. 67: 1401–1410.

CAMPANA, S. E., AND P. C. F. HURLEY. 1989. An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 46: 603–613.

CAMPANA, S. E., S. J. SMITH, AND P. C. F. HURLEY. 1989a. An age-structured index of cod larval drift and retention in the waters off of Southwest Nova Scotia. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 191: 50–62.

1989b. A drift-retention dichotomy for larval haddock (*Melanogrammus aeglefinus*) spawned on Browns Bank. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 000–000.

CAMPANA, S. E., K. T. FRANK, P. C. F. HURLEY, P. A. KOELLER, F. H. PAGE AND P. C. SMITH. 1989c. Survival and abundance of young cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): (This issue).

COLTON, JR., J. B., W. G. SMITH, A. W. KENDALL, JR., P. L. BERRIEN, AND M. P. FAHAY. 1979. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. Fish. Bull. 76: 911–915.

DRINKWATER, K. F., AND R. W. TRITES. 1987. Monthly means of temperature and salinity in the Scotian Shelf region. Can. Tech. Rep. Fish. Aquat. Sci. 1539: iv + 101 p.

FRIDGEIRSSON, E. 1978. Embryonic development of five species of gadoid fishes in Icelandic waters. Rit Fiskideildar 5: 1–40.

Gagné, J. A., and R. N. O'Boyle. 1984. The timing of cod spawning on the Scotian Shelf. p. 501–517. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flodevigen Rapportser 1.

Grosslein, M. D., and R. C. Hennemuth. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 194: 77–88.

Homans, R. E. S., and V. D. Vladykov. 1954. Relation between feeding and the sexual cycle of the haddock. J. Fish. Res. Board Can. 11: 535–542.

Kohler, A. C. 1960. The growth, length–weight relationship, and maturity of haddock (*Melanogrammus aeglefinus* L.) from the region of Lockeport, N.S. J. Fish. Res. Board Can. 17: 41–60.

Koslow, J. A., S. Brault, J. Dugas, and F. Page. 1985. Anatomy of an apparent year-class failure: the early life history of the 1983 Browns Bank haddock (*Melanogrammus aeglefinus*). Trans. Am. Fish. Soc. 114: 478–489.

Lawrence, D. J., and R. W. Trites. 1983. Surface oil spill trajectory modelling for Georges and Browns Banks. Can. Tech. Rep. Hydrogr. Ocean. Sci. 29: iv + 30 p.

Marak, R. R., and J. B. Colton, Jr. 1961. Distribution of fish eggs and larvae, temperature and salinity in the Georges Bank–Gulf of Maine area, 1953. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 398: 1–61.

Markle, D. F., and L. A. Frost. 1985. Comparative morphology, seasonality, and a key to planktonic fish eggs from the Nova Scotian Shelf. Can. J. Zool. 63: 246–257.

McKenzie, R. A. 1940. The spring haddock "run," Jordan Harbour, N.S. Fish. Res. Board Can. Atlant. Prog. Rep. 28: 9–13.

Neilson, J. D., E. M. DeBlois, and P. C. F. Hurley. 1988. Stock structure of Scotian Shelf flatfish as inferred from ichthyoplankton survey data and the geographic distribution of mature females. Can. J. Fish. Aquat. Sci. 45: 1674–1685.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 183: 27–40.

Page, F. H., and K. T. Frank. 1989. Spawning time and egg duration in haddock stocks of the northwest Atlantic. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 000–000.

Perry, R. I., and P. C. F. Hurley. 1986. Circulation and potential ichthyoplankton dispersal in the Gulf of Maine, Browns and Georges Bank areas. CAFSAC Res. Doc. 86/37: 16 p.

Scott, J. S. 1983. Inferred spawning areas and seasons of groundfishes on the Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 1219: iii + 14 p.

Serebryakov, V. P. 1971. On haddock spawning in the Northwest Atlantic area. Int. Comm. Northw. Atlant. Fish. Redbook 1971, Part III: 83–91.

Sherman, K., W. G. Smith, J. R. Green, E. B. Cohen, M. S. Berman, K. A. Marti, and J. R. Goulet. 1987. Zooplankton production and the fisheries of the northeastern shelf, p. 268–282. *In*: R. H. Backus [ed.] Georges Bank. The MIT Press, Cambridge.

Smith, P. C. 1983. The mean and seasonal circulation off southwest Nova Scotia. J. Phys. Oceanogr. 13: 1034–1054.

1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

Smith, W. G., and W. W. Morse. 1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. Mar. Ecol. Prog. Ser. 24: 1–13.

van Guelpen, L., D. F. Markle, and D. J. Duggan. 1982. An evaluation of accuracy, precision and speed of several zooplankton subsampling techniques. J. Cons. Int. Explor. Mer 40: 226–236.

Waiwood, K. G., and M.-I. Buzeta. 1989. The reproductive biology of Southwest Scotian Shelf haddock (*Melanogrammus aeglefinus* L.). Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): 000–000.

Spatial Comparison of Recent Growth in Postlarval Atlantic Cod (*Gadus morhua*) off Southwestern Nova Scotia: Inferior Growth in a Presumed Nursery Area[1]

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Suthers, I. M., K. T. Frank, and S. E. Campana. 1989. Spatial comparison of recent growth in postlarval Atlantic cod (*Gadus morhua*) off southwestern Nova Scotia: inferior growth in a presumed nursery area. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 113–124.

Spatial variation in distribution, age, and recent growth of postlarval cod (*Gadus morhua*) were examined off southwestern Nova Scotia during the early summer of 1985 and 1986. Ages ranged between 40–120 d posthatch throughout the sampling area, from the spawning grounds on Browns Bank, to nearshore (<55 m depth) and offshore regions 150 km north. The hatch-date distributions during 1986 between cruises 3 wk apart were significantly different in the nearshore, contrary to the age structure on the Bank which appeared more stable. These observations are consistent with retention of cod in the Browns Bank gyre, coupled with episodic leakage and northerly advection in the residual current. Recent growth determined from otolith increment widths was significantly less for those cod sampled at nearshore stations than for cod offshore and on the Bank. Recent growth was significantly correlated with zooplankton biomass in a size range suitable for postlarval cod, while sea temperature was correlated in only one cruise. Nearshore areas had on average 25% of the zooplankton biomass found on the Bank. Recent growth indices of the third and fourth week precapture were not significantly different between the nearshore and offshore, implying that the cod had shared a common environment, and common origin such as Browns Bank.

Les variations spatiales dans la répartition, l'âge et la croissance récente des morues post-larvaires (*Gadus morhua*) ont été étudiées au large du sud-ouest de la Nouvelle-Écosse au début de l'été de 1985 et de 1986. Les âges variaient entre 40 et 120 jours après l'éclosion dans toute la région d'échantillonnage, puis les aires de fraye dans le banc Browns jusqu'à l'avant-plage (55 m de profondeur) et les régions du large à 150 km au nord. Les distributions des dates d'éclosion en 1986 entre les expéditions espacées de 3 sem étaient très différentes dans l'avant-plage, contrairement à la structure d'âge sur le banc, qui semblait plus stable. Ces observations concordent avec le phénomène de retenue des morues dans le tourbillon du banc Browns, couplé aux pertes épisodiques et à l'advection vers le nord des courants résiduels. La croissance récente déterminée à partir de la largeur de l'otolithe était considérablement inférieure chez les morues échantillonnées dans les stations d'avant-plage par rapport aux morues du large et du banc. La croissance récente affichait une corrélation significative avec la biomasse de zooplancton dans la gamme de taille qui convient à la morue post-larvaire, tandis que la température de l'eau n'a pu être correliée que pour une seule expédition. Les zones d'avant-plage affichaient en moyenne une biomasse de zooplancton équivalente à 25 % de celle du banc. Les indices de croissance récente relevés pendant les troisième et les quatrième semaines précédant la capture ne différaient pas considérablement dans l'avant-plage et au large, ce qui signifie que la morue a partagé un environnement commun et une origine commune, tels que le banc Browns.

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The dispersal of marine planktonic fish eggs and larvae has been viewed as a process serving to enhance the survival of postlarvae by increasing the probability of encountering abundant food (Norcross and Shaw 1984; Doherty et al. 1985), and/or decreasing the risk of predation (Johannes 1978; Zijlstra 1988). Such areas are commonly referred to as nursery grounds and represent the end point of the dispersal process (Harden Jones 1968; Checkley et al. 1988). Many marine fishes, including Atlantic cod (*Gadus morhua*), spawn offshore while their postlarvae and juveniles can occur in nearshore and estuarine areas (Daan 1978; Pihl 1982; Gødo and Sunnanå 1984; Lear and Wells 1984; Riley and Parnell 1984; MacDonald et al. 1984; Tremblay and Sinclair 1985; Suthers and Frank 1989). Pelagic juvenile cod also occur offshore (Zijlstra 1988), and the consequences for their growth and survival in the nearshore and offshore environments are unknown.

In southwestern Nova Scotia, residual currents flow northwards from Browns Bank (a major spawning area for cod) toward the coast. In the spring of 1985–87, high concentrations of postlarval and pelagic juvenile cod occurred on Browns Bank, as well as landward of the 55-m isobath (Suthers and Frank 1989). As there was no discernible larval size gradient between Browns Bank and the inshore areas, the distribution of pelagic juvenile cod appeared to be influenced by processes of both northerly drift in the residual current and retention on the natal bank, while the occasional high inshore abundance of postlarval cod was suggested to be indicative of a nursery ground (Suthers and Frank 1989).

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Dispersal from the spawning area to potential nursery grounds is contrary to conclusions from large-scale ichthyoplankton surveys on the Scotian Shelf, that eggs and larvae of groundfish are retained in tidally induced gyres associated with the major offshore banks (Gagné and O'Boyle 1984; O'Boyle et al. 1984; Neilson et al. 1988). Larval retention in a geographically predictable area was argued to be the principal factor regulating success of a stock, rather than favourable growth and survival conditions that might be found in a nursery ground (Iles and Sinclair 1982; Sinclair and Tremblay 1984; Sinclair and Iles 1985). A functional role of nursery grounds can be objectively assessed from condition indices of the postlarvae, or from estimates of growth (Theilacker 1986; Townsend et al. 1987; Buckley and Lough 1987).

This paper extends upon the geographic analysis of larval and postlarval cod size distributions off southwestern Nova Scotia contained in Suthers and Frank (1989), by determining the spatial distribution of age and recent growth in the early summer of 1985 and 1986. Age is an exact measure of larval duration and superior to larval length estimates for examining the dispersal process. We examine the hypothesis that passive drift from the spawning grounds to the nearshore environment typifies the dispersal process of cod yielding older cod inshore relative to those on Browns Bank. Postlarvae from the nearshore were also predicted to exhibit higher growth rates assuming that the inshore environment was a functional nursery ground. We test this hypothesis using a model of recent growth, incorporating food abundance and sea temperature which are the principal determinants of otolith growth in fish (Campana and Neilson 1985; Jones 1986). Recent growth was assessed using the width of the peripheral daily growth increments of the otolith.

Methods

Study Area, Cruise Dates and Sampling Gear

Three ichthyoplankton surveys were conducted during the spring and early summer of 1985 and 1986 in the nearshore and shelf waters of southwestern Nova Scotia over an area of approximately 650 km^2 (Fig. 1). The region is dominated by strong semi-diurnal tides, with a residual current flowing north from Browns Bank (5–10 km·d^{-1}). A persistent clockwise gyre is situated over the western cap of Browns Bank, with a residence time of 5–25 d (Greenberg 1983; Smith 1983, 1989).

To assess spatial variation in the abundance and age of cod the survey area was divided into four transverse regions and a fifth region to the east (Fig. 1). Region 1 included Browns Bank, which is the principal late winter–early spring cod spawning ground in the area (O'Boyle et al. 1984; Campana and Hurley 1989), and all other stations south of 43.00°N. Regions 2, 3 and 4 were to the north and were divided into inshore (<55 m station depth) and offshore components. In cruise 86-3, region 5 was included, east of 65.00°W (Fig. 1).

During the May 1985 survey, two cruises were conducted at the same time (Table 1). Cruise 85-1 sampled the offshore waters and cruise 85-2 sampled the nearshore (Fig. 1). During cruise 85-1, a Tucker trawl (2 × 2.5 m mouth opening, 1600-μm mesh) was the principal sampling gear. A complete description of this gear type and deployment scheme is contained in Suthers and Frank (1989). In cruise 85-2, a 1.0-m diameter ring net (1000-μm mesh) was towed from the surface to 5 m at 2 m·s^{-1} for 15 min; filtering approximately 1000 m^3. An electronic package towed beneath the net recorded temperature, depth, and towing speed while a TSK (Tsurumi-Seike Co. Ltd) flow meter in the mouth of the net recorded volume filtered.

During the May 1986 survey, cruises 86-1 and 86-2 were conducted during the same time period (Table 1). A Tucker trawl was used at all sampling locations.

In June 1986 (cruise 86-3, Table 1) we sampled the nearshore and offshore with a Tucker trawl with a deployment scheme identical to that in cruise 86-2. Salinity and temperature were determined at the end of the tow with bottle collections and a temperature-depth probe.

Samples from all cruises were preserved in 5% formalin in fresh water, buffered with sodium borate. Within 3–10 d, postlarval cod were transferred to 95% ethanol to preserve the otoliths. All cod were counted and measured (standard length, SL) to the nearest 0.2 mm. Lengths were not corrected for preservation shrinkage.

Zooplankton Collection and Analysis

Zooplankton biomass data for cruises 85-1 and 86-1 (Table 1) were taken from Frank (1988). Zooplankton was collected at each station with a mini-BIONESS (0.25 m^2 mouth opening, 333-μm mesh). The three most northerly stations in cruise 85-1 were not sampled, so zooplankton biomass (Y, milligrams per cubic metre) was estimated from distance offshore (X, kilometres) using the equation

$$\ln Y = (1.02) \times \ln X - 1.33, \text{ after Frank (1988).}$$

Zooplankton was sampled during cruises 85-2, 86-2, and 86-3 with a 0.5-m diameter, 405-μm mesh ring net (Table 1). Macrozooplankton (jellies, euphausiids) was excluded by rinsing the sample through a 4 or 10-mm mesh sieve before preservation in 5% formalin in freshwater. In the laboratory, zooplankton was divided by sieving into four size fractions; 308–602, 602–860, 860–1050, and >1050 μm. Total zooplankton biomass (principally calanoid copepods, small euphausiids) was estimated as the sum of dry weight fractions, expressed as milligrams per cubic metre.

Otolith Analysis

Cod otoliths form one growth increment per day although two to three narrow increments around the nucleus may go unresolved (Bolz and Lough 1988; Campana and Hurley 1989). All otoliths were polished with lapping film to the nuclear plane and the number of daily increments counted at 1250× magnification (Campana and Neilson 1985). Each otolith was counted three to six times until a consistent age was obtained. If any of the counts differed by more than 10, often on account of poor sample preparation, the otolith was discarded (approximately 6% overall). Increment widths and otolith radius (Fig. 2) were measured on a video screen using an image analysis system (Campana 1987). The most recent, outer increment was

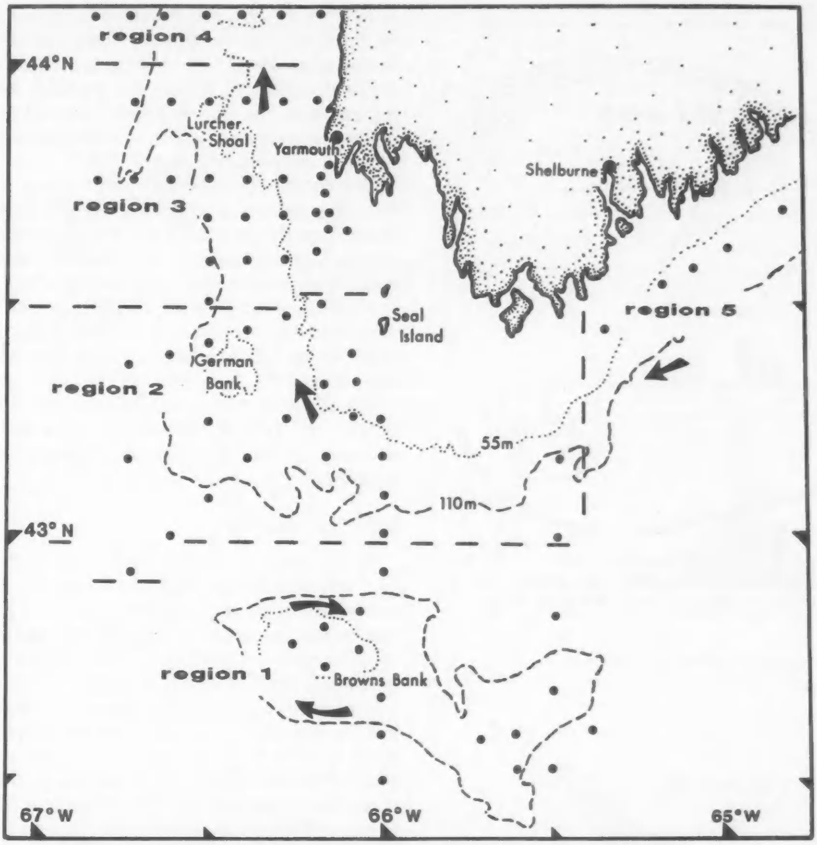


FIG. 1. Stations sampled off southwestern Nova Scotia during May 1985, 1986 and June 1986, and division into five regions. The 55-m isobath (dotted) delineates the offshore from the nearshore. Arrows indicate the mean circulation (Greenberg 1983; Smith 1983).

TABLE 1. Cruise information pertaining to the three survey periods. i = inshore. Key to gear deployed; BN, BIONESS; HM, 0.5-m diameter ring net; 1m, 1.0-m diameter ring net; Tt, Tucker trawl.

Survey	Cruise	Dates	Gear deployed	Stations	Regions covered	Zooplankton sampling gear
May 1985	85-1	9–21 May	Tt	30	1,2,3	BN
	85-2	16–22 May	1m	8	3i	HM[a]
May 1986	86-1	10–18 May	Tt	34	1,2	BN
	86-2	14–23 May	Tt	20	2i	HM
June 1986	86-3	5–11 June	Tt	49	1,2i,3i,4i,5	HM

[a] Average of 10 neighbouring stations.

usually incomplete and was not included in the analysis. The left and right lapilli of 23 cod were analysed to compare the age and increment width measurements. The average difference in age was 7% (range 0–26%) and the average difference in width of the outer 14 increments was 8.6% (range 0–26%).

All cod from cruises 85-1 and 85-2 were aged, using one of the pair of lapillar otoliths chosen at random. The ages and increment widths of cod sampled with the 1.0-m diameter ring net in cruise 85-2 were analysed with the Tucker trawl samples of cruise 85-1 as there was no significant difference in the age–length relationship (analysis of covariance, ANCOVA $p>0.5$). Poor preservation of the otoliths at one station in region 3 (cruise 85-1), primarily included those from cod <15 mm standard length (SL). Therefore an age–length regression from cruise 85-1 was used to estimate the probable age distribution of these smaller fish for region 3 ($\text{age} = 39.6 \times \ln(\text{SL}) - 40.6$, $r^2 = 0.71$).

During 1986, when pelagic juvenile cod were abundant, samples were selected for otolith analysis from stations within regions (Fig. 1) where the greatest densities were recorded.

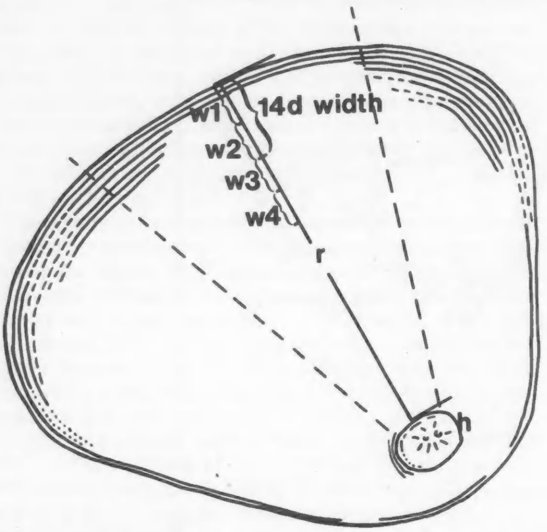


FIG. 2. Diagram of lapillar otolith showing the location of the measurements taken. Measurements were confined to the area between the dashed lines and include: 14-d width, r = radius, h = hatch check, w1–w4 are the 7-d widths.

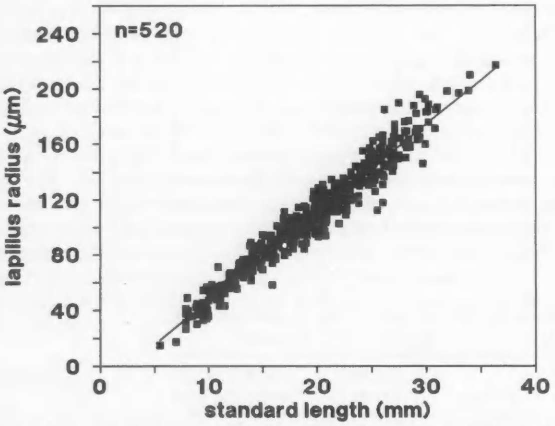


FIG. 3. Linear relationship of lapillus radius (μm) on standard length (mm) for all cruises. The intercepts between cruises were significantly different. Individual cruise regressions: 85-1,2 radius = $-19.82+6.40\times SL$ $r^2=0.92$; 86-1 radius = $-6.85+5.82\times SL$ $r^2=0.95$; 86-2 radius = $-16.67+6.50\times SL$ $r^2=0.96$; overall radius = $-16.08+6.34\times SL$ $r^2=0.95$.

Occasionally when the station sample sizes exceeded 15 individuals, a random subsample was taken.

In this study, the otolith radius was linearly related to the SL over all cruises (Fig. 3). The slopes were not significantly different among cruises but the intercepts were different ($p<0.001$). Within a cruise the otolith radius–SL regressions were not significantly different among regions (ANCOVA $p>0.3$), except for region 2 inshore, cruise 86-2 ($p<0.01$). The regression equation for this region was radius $= 6.66\times SL-23.39$ ($r^2=0.95$). Therefore any increase in otolith radius (i.e. a daily growth increment) of cod in this region would not reflect the same proportional increase in SL as in other regions, and therefore increment widths for cruises 86-1,2 could not be directly compared between regions as indices of recent growth. A corrected radius was calculated for region 2 inshore by adding the residuals from the radius–SL regression, to the estimated radius derived from the radius–SL regression of regions 1 and 2. The increment widths were altered proportionally (from −5 to +25%).

The cumulative width of the 14 recent growth increments prior to capture was used as an index of recent growth. While otolith size and fish size are strongly correlated, daily otolith growth rate is believed to be a running average of fish growth under average environmental conditions (Fig. 3; see Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989). The metabolic lag between daily feeding and otolith growth is unknown for cod, although in salmon parr it is 1–2 wk (Wilson and Larkin 1982; Volk et al. 1984). Consequently the summed widths of the 14 most recent daily growth increments was used in this study, both as a conservative measure of recent growth, and as a growth index for the regions where the cod were sampled.

Statistical Analyses

As the cruises extended over 6–10 d, each age was adjusted to a common capture date, corresponding to the mid-date of the cruise (maximum adjustment was ±4 d). Where regional sample sizes exceeded 30 fish, the regional age frequency histograms were compared with a Kolmogorov-Smirnov test. The probability level of significance for the multiple comparisons was adjusted to $0.05/n$ where n was the number of regions. To test for regional differences in recent growth rate, the cumulative width of the 14 most recent complete daily growth increments for each cruise (Fig. 2) was analysed in two ways, both of which incorporated size (SL) to remove its effect. Inclusion of age in the model did not result in a significant increase in the variance explained and therefore was not included in any of the models. The first test was a linear model to examine the effect of regions on the cumulative 14-d increment width. The second test was a multiple regression model of the cumulative 14-d increment width, as a function of zooplankton and sea surface temperature (1–5 m below surface). This test assumes that food and temperature recorded at capture was representative of the previous 14 d. For each cruise the four outer 7 d widths (Fig. 2) were analysed separately as in the first test above, to examine the effect of regions on the growth history. Variances of otolith increment widths, SL and environmental variables used in these models were not homogeneous (Cochran's C), requiring logarithmic transformations. Residuals in both models were normally distributed. All analyses were performed using SYSTAT (Systat Inc. 1988, Evanston, Il.).

Results

Spatial Distribution in Abundance

Over 80% of the total catch of postlarval cod (>10 mm SL) occurred north of Browns Bank in regions 2 and 3 in May 1985 and 1986 (Suthers and Frank 1989; Fig. 4a and 5a). In May 1985, cod were particularly abundant (>10 per 1000 m^3) in region 3 inshore (3i). In June 1986 (cruise 86-3), conducted 3 wk later than cruises 86-1,2 pelagic juvenile cod were concentrated on Browns Bank, and in region 3i — although sampling was limited offshore in region 2 (Fig. 6a). For the 31 stations common to cruises 86-1,2 and 86-3, there was no

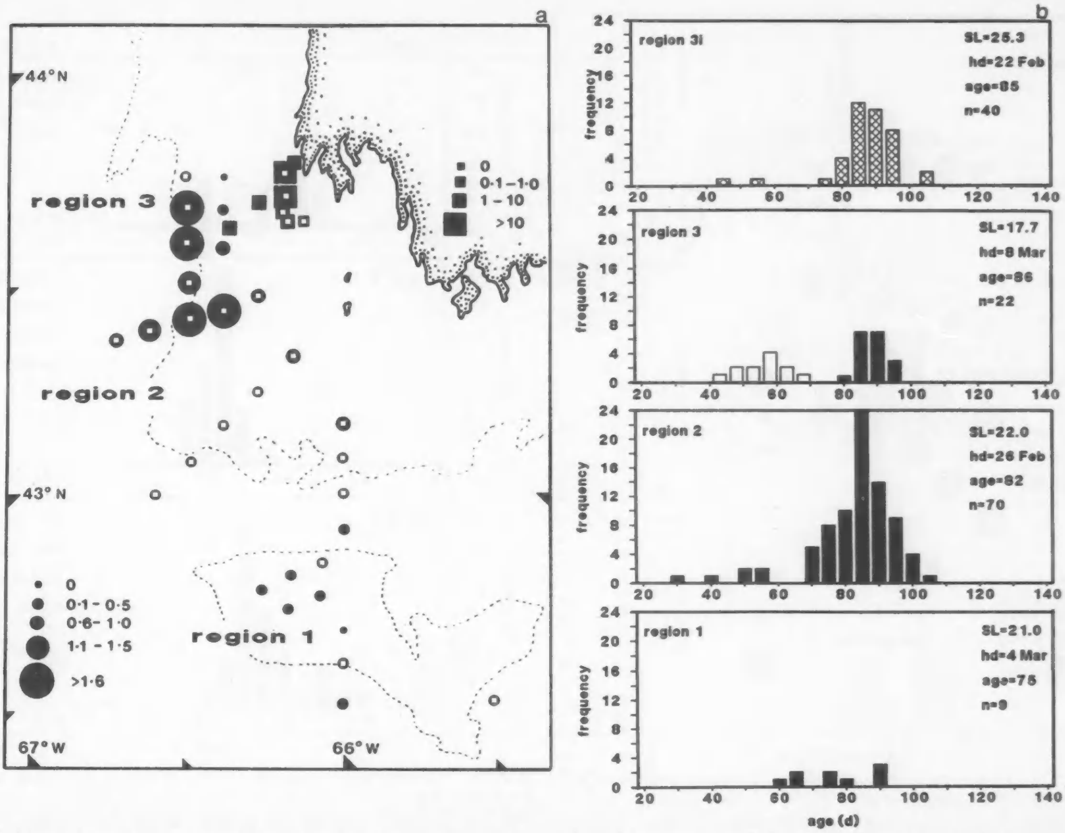


FIG. 4. (a) Expanding symbol plot of postlarval cod concentration (No.·1000 m^{-3}) during cruise 85-1 (circles, data from Suthers and Frank 1989) and during cruise 85-2 (squares). Note different concentration scales for the two cruises. Symbols containing a white square show location of samples used in the age and growth analysis. (b) Regional age frequency histograms adjusted to a common sampling date, 18 May. Cross-hatched histogram refers to cod sampled with the 1.0-m ring net. Open histogram indicates age frequency estimated from length frequency (see Methods). Probability value associated with Kolmogorov-Smirnov comparison of age frequency distributions between regions 2,3i = 0.9. Also shown are regional average standard length (SL), hatch date (hd), age, and sample size.

significant correlation in cod concentration (Spearmans rank correlation $r_s = 0.13$, $p > 0.05$). There was no apparent size gradient from region 1 to region 4i during cruise 86-3, which was also demonstrated in other cruises (Suthers and Frank 1989).

Spatial Distribution of Ages

The age distributions between regions 1, 2, 3, and 3i during cruise 85-1,2 (adjusted to a common capture date, 18 May) showed no gradient in age from Browns Bank to inshore (Fig. 4b). There was no significant difference between the age frequency histograms of region 2 and 3i (Kolmogorov-Smirnov test $p > 0.9$).

During cruises 86-1,2 (Fig. 5b), the age frequency histogram of region 2 was different from regions 1 ($p < 0.001$) and 2i ($p < 0.001$) which, in turn, were not significantly different from each other ($p = 0.94$). Thus cod in region 2 were significantly older with the mean age greater by 10 d — although the age distribution in region 2i appeared polymodal (Fig. 5b).

The age distributions 3 wk later during cruise 86-3 were significantly different between region 1 compared with regions 2i and 5 — to the north and northeast ($p < 0.03$, Fig. 6b). Region 2i was different from region 3i ($p < 0.04$), and region 3i was different from region 5 ($p = 0.01$). Overall, postlarvae in regions 1 and 3i were 10 d older than the other regions, although again the age distributions tended to be polymodal.

Two regions were sampled in cruises 86-1,2 and again in cruise 86-3, permitting an assessment of the similarity of the age structure between regions over the intervening 3 wk. The hatch date distributions for region 1 did not differ significantly between cruises (Fig. 7a and b, Kolmogorov Smirnov test $p = 0.06$), showing a similar range, from early March to mid April (although the distribution appeared polymodal in cruise 86-3). In contrast, the hatch date distribution of region 2i was significantly different between the two cruises (Fig. 7c and d, $p < 0.001$), with later spawned postlarvae appearing in June. The hatch dates at region 2i ranged from mid February to mid April during cruise 86-2 and from mid March to early May in cruise 86-3.

Index of Recent Growth

The index of recent growth was initially analysed with an ANCOVA model (Table 2a), with region a factor and SL a covariate. The slopes of the recent growth index on SL during

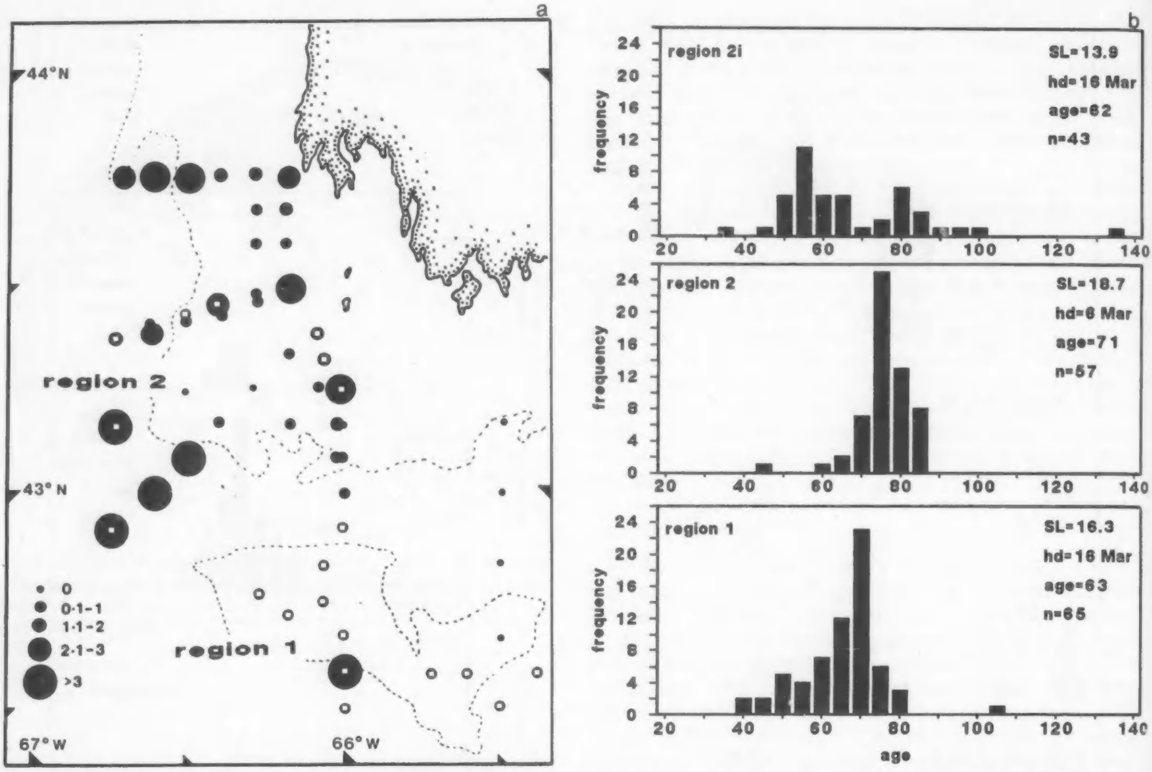


FIG. 5. (a) Expanding symbol plot of postlarval cod concentration (No.·1000 m^{-3}) during May, cruises 86-1,2 (from Suthers and Frank 1989). Symbols and abbreviations as in Fig. 4. (b) Corresponding regional age frequency histograms adjusted to a common sampling date, 18 May. Probability values associated with Kolmogorov-Smirnov comparisons of age frequency distributions between regions 1,2<0.001; region 2,2i = 0.001; region 1,2i = 0.94.

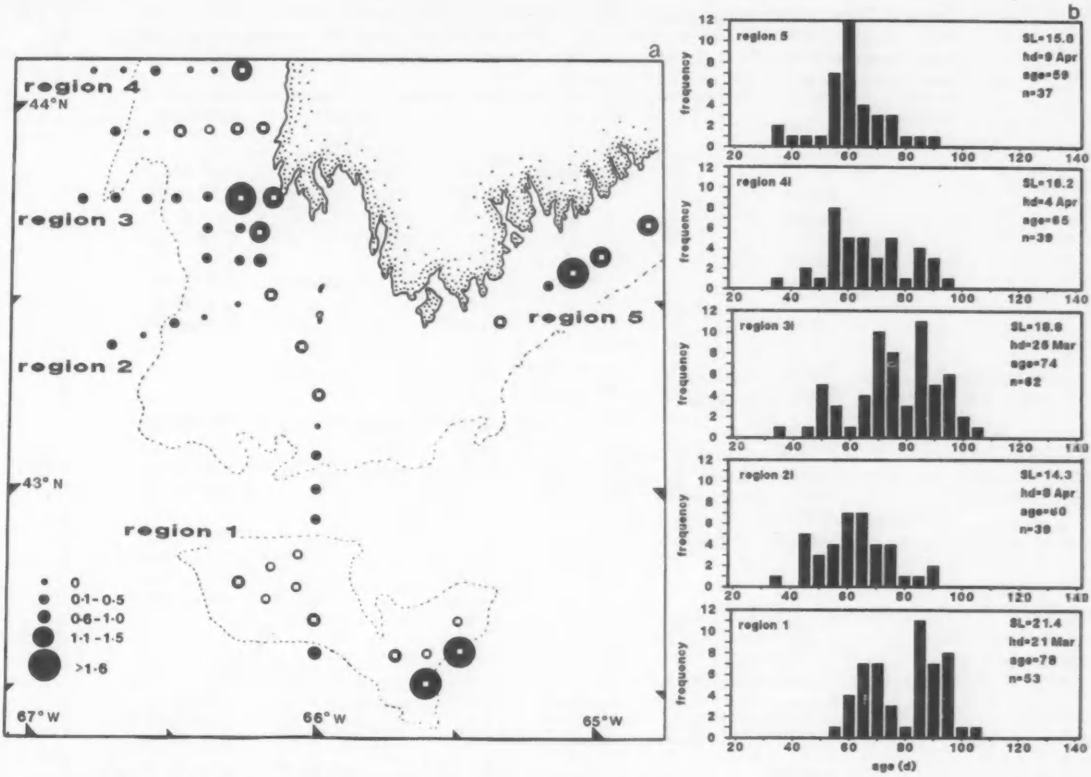
May 1985 were significantly greater in regions 1, 2, and 3 than in region 3i (Table 2a, Fig. 8a). For example, offshore cod 25 mm SL grew approximately 25% over the previous 2 wk, compared with 22% inshore. During cruises 86-1,2 the slopes from Browns Bank and region 2 offshore were the same, and significantly greater from that of cod from region 2i (Table 2a, Fig. 8b). Thus in May 1986, 25 mm SL cod offshore grew approximately 33% over the previous 2 wk, compared with 23% inshore. Three weeks later during cruise 86-3, region 1 had the greater slope (Table 2a, Fig. 8c), and was significantly different from the inshore regions. At this time 25 mm SL cod in region 1 grew approximately 29% over the previous 2 wk compared with 24% inshore.

The second model used was a multiple regression model of the recent growth (Table 2b), incorporating SL, total zooplankton (>308 μm) and sea temperature (between 1 and 5 m deep) at each station as independent variables. Total zooplankton concentration and sea temperature were selected because they were considered to have the greatest effect on increment width (Campana and Neilson 1985) and were the least confounded by collinearity.

The multiple regression model explained almost as much of the variance in the recent growth index as the ANCOVA model (Table 2b). The influence of the region factor identified in the ANCOVA model was removed, as the region by region residuals from the multiple regression of each cruise were not significantly different from zero, except for cruise 85-2, region 3i. This exception may be explained by the disparate regional sample sizes, and perhaps the use of a mean zooplankton value for cruise 85-2 (see Table 1). Total zooplankton concentration was significantly and positively correlated with recent growth in all cruises after size was entered into the multiple regression. Sea surface temperature was significantly and positively correlated only in cruises 86-1,2 (Table 2b).

The slope of the recent growth index-SL for each region, and regional average total zooplankton biomass were positively related (Fig. 9). Region 2 and 3 (offshore) and Browns Bank had the greatest zooplankton concentration, tending to form an offshore grouping, distinct from the nearshore. The nearshore had less than 25% of the zooplankton biomass concentration of Browns Bank (Fig. 9).

The four 7-d indices of growth (Fig. 2) were analysed with region as a factor and SL a covariate (identical to the first model above). The increments became narrower and often indistinct towards the nucleus in some specimens, so the sample size was reduced (cruises 85-1,2 95% of the original sample; cruises 86-1,2 72%; cruise 86-3 67%). The SL was back calculated for each week using the cruise otolith radius–SL regression. Analysis of the most recent 7-d otolith growth prior to capture generally showed similar results as the 14-d index except for cruises 85-1,2, which showed there was no effect of regional difference in slopes, although the intercepts were significantly different among regions (Table 3). Overall, the two most recent 7-d widths showed significant effects of region (Table 3), shown in


a
region 4
44°N
region 3
region 2
region 5
43° N
region 1
0
0·1-0·5
0·6-1·0
1·1-1·5
>1·6
67° W
66° W
65° W
b
region 5
SL=15.8
hd=9 Apr
age=59
n=37
region 4i
SL=16.2
hd=4 Apr
age=65
n=39
region 3i
SL=18.8
hd=26 Mar
age=74
n=62
region 2i
SL=14.3
hd=8 Apr
age=60
n=39
region 1
SL=21.4
hd=21 Mar
age=78
n=53
frequency
age (d)
0
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12
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60
80
100
120
140

FIG. 6. (a) Expanding symbol plot of postlarval cod concentration (No.·1000 m^{-3}) during June, cruise 86-3. Symbols and abbreviations as in Fig. 4. (b) Corresponding regional age frequency histograms adjusted to a common sampling date, 7 June (20 d after 18 May for comparison with cruises 85-1,2 and 86-1). Probability values associated with Kolmogorov-Smirnov comparisons of age frequency distributions between regions 1,2i = 0.03; region 1,3i = 0.99; region 1,4i = 0.23; region 1,5 = 0.004; region 2i,3i = 0.04; region 2i,4i = 0.99; region 2i,5 = 0.99; region 3i,4 = 0.31; region 3i,5 = 0.01; and region 4i,5 = 0.99.

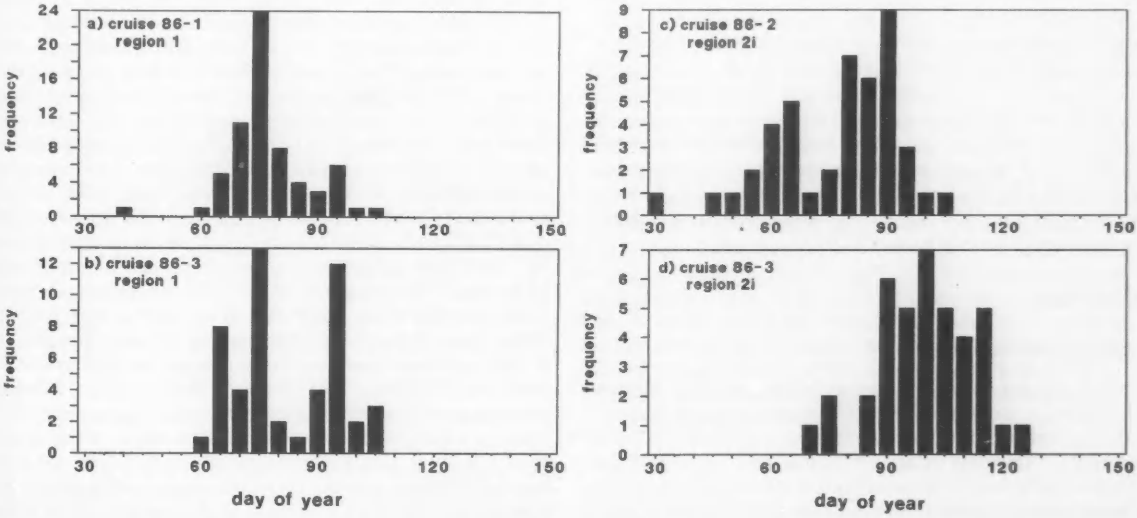

FIG. 7. Hatch date frequency distributions of cod. (a) Cruise 86-1, region 1, (b) cruise 86-3, region 1, (c) cruise 86-2, region 2i, (d) cruise 86-3, region 2i.

TABLE 2. Linear models and parameter estimates resulting from the analysis of the most recent 14-d width of the otolith for each cruise. a) width = constant + region + SL + region × SL b) width = constant + SL + Z + T; SL = standard length, T = sea surface temperature, Z = zooplankton biomass concentration. * $0.005<p<0.05$, ** $p<0.005$.

Cruises	Source	SS	df	MS	r^2	Parameter	Coefficient (*SE*)
85-1,2	(a) SL	1.47	1	1.47**	0.66	region (1) × SL	1.03 (0.17)
	Region	0.09	3	0.03	0.07	region (2) × SL	0.96 (0.07)
	Region × SL	0.12	3	0.04*	0.02	region (3) × SL	1.15 (0.17)
	Error	1.91	131	0.01		region (3i) × SL	0.68 (0.08)
	Model				0.75		
	(b) Constant				0	constant**	0.81 (0.20)
	SL				0.66	SL**	0.87 (0.05)
	Z				0.04	Z**	0.08 (0.02)
	T				0	T	−0.10(0.08)
	Model	5.28	3	1.48**	0.70		
	Error	2.26	135	0.02			
86-1,2	(a) SL	4.37	1	4.37**	0.71	region(1) × SL	0.88 (0.06)
	Region	0.27	2	0.14**	0.05	region (2) × SL	0.86 (0.08)
	Region × SL	0.37	2	0.19**	0.04	region(2i) × SL	0.46 (0.07)
	Error	1.95	145	0.01			
	Model				0.80		
	(b) Constant				0	constant**	0.86 (0.15)
	SL				0.71	SL**	0.72 (0.04)
	Z				0.03	Z**	0.03 (0.01)
	T				0.03	T**	0.29 (0.07)
	Model	7.60	3	2.53**	0.77		
	Error	2.26	147	0.02			
86-3	(a) SL	4.35	1	4.35**	0.62	region(1) × SL	0.79 (0.07)
	Region	0.41	4	0.10*	0.01	region(2i) × SL	0.46 (0.05)
	Region × SL	0.46	4	0.12*	0.04	region(3i) × SL	0.39 (0.06)
	Error	3.62	192	0.02		region(4i) × SL	0.46 (0.10)
	(b) Constant				0	constant**	1.41 (0.39)
	SL				0.62	SL**	0.56 (0.03)
	Z				0.02	Z**	0.02 (0.01)
	T				0	T	0.24 (0.19)
	Model	7.05	3	2.35**	0.64		
	Error	4.05	198	0.02			

Fig. 10 by the different adjusted regional mean widths (cruises 85-1,2) and the width–SL slopes (cruises 86-1,2, 86-3). The regional differences reflect the zooplankton biomass characteristics shown above, yet these differences are not maintained in the growth history record of the otolith. The regional differences in all cruises decreased until they were not significantly different by the third and fourth week precapture (Fig. 10). However, cod from region 5, cruise 86-3 tended to show slower growth over the third and fourth weeks precapture compared with the other regions, suggesting these fish were immigrants from outside the study area (Fig. 10c).

Discussion

Age Distribution and Dispersal

The complex spatial distribution of postlarval age between the spawning grounds on Browns Bank and regions to the north confirm earlier analyses of size (Suthers and Frank 1989) and larval age (Campana et al. 1989), that both larval drift and retention influence the dispersal patterns of cod in southwestern Nova Scotia. At residual current speeds of 5–10 km·d^{-1} (Smith 1989), cod 100–150 km from the Bank should have been 2–4 wk older than those on the Bank. Regional differences in age were apparent, but were neither large (difference in mean age < 10 d) nor consistent with the direction of the residual flow. The hypothesis that passive, uniform drift occurs from the spawning grounds to the nearshore environment was rejected, because of the lack of an age gradient. The northerly distribution of postlarval cod, and the lack of correlation in the horizontal distribution of postlarval cod between May and June of 1986 is taken as evidence to reject the hypothesis of larval cod retention in geographically discrete areas (O'Boyle et al. 1984; Gagné and O'Boyle 1984). Periodic breakdown of the Browns Bank gyre (Smith 1989) could influence eggs, larvae, and postlarvae by a northward drift causing a variable residence time of cod on the Bank. The persistence of 60–100 d old cod near Browns Bank and their broad distribution to the north during June of 1986, agrees with this interpretation. An alternative hypothesis is that nearshore spawning could obscure an age gradient. Hurley and Campana (1989) showed that between 1983–85, nearshore spawning off southwestern Nova Scotia was relatively minor in comparison to the offshore. The results of the recent growth analysis also show that growth of nearshore cod was less than offshore, with a common offshore growth history (Fig. 10).

The partial retention of the postlarval cod population on the Bank during 1986 was confirmed by the relative stability in the

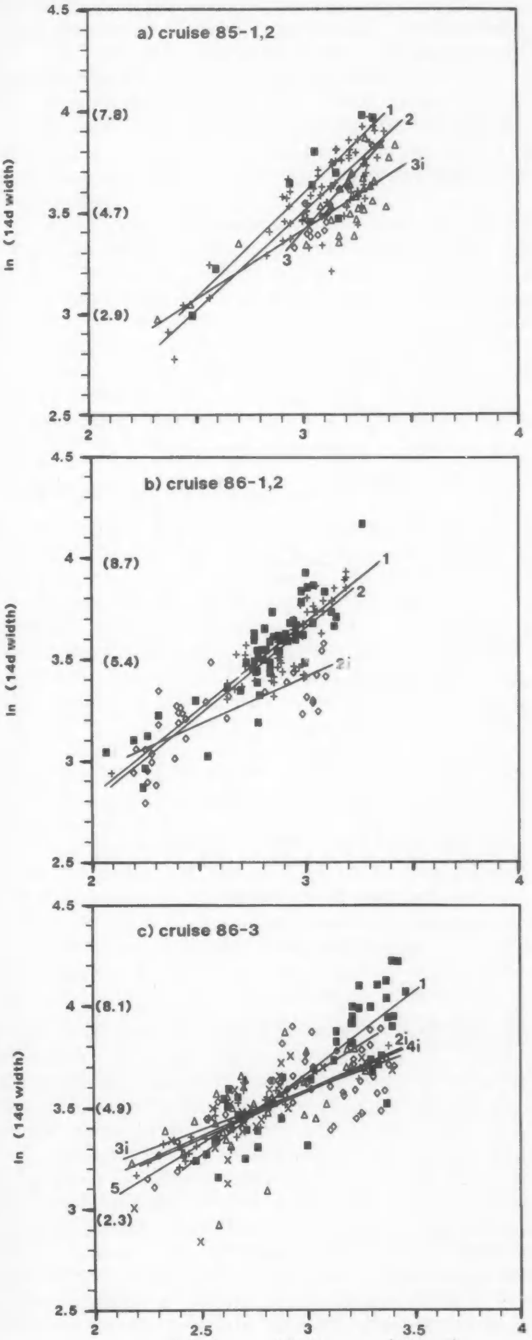

FIG. 8. Log–log plot of the cumulative width of the most recent 14 daily increments on standard length (SL) for each region during (a) cruises 85-1,2; region 1 (■), region 2 (+), region 3 (◇), region 3i (Δ), (b) cruises 86-1,2; region 1 (■), region 2 (+), region 2i (◇), and (c) cruise 86-3; region 1 (■), region 2i (+), region 3i (◇), region 4i

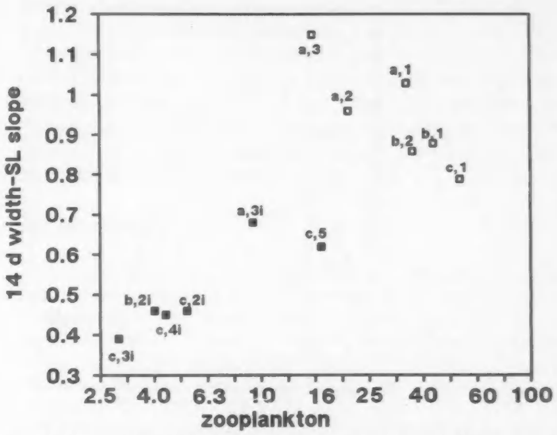

FIG. 9. Scatter plot of the 14-d width–SL slope (from Table 2a), and regional average biomass (log scale, mg·m^{-3}) of total zooplankton (>308 μm) during cruises (a) 85-1,2; (b) 86-1,2 and (c) 86-3. Points are identified as cruise, region. Closed symbols; inshore stations <55 m, including region 5, open symbols; offshore stations including Browns Bank.

TABLE 3. Comparison of levels of significance for the region factor (cruise 85-1,2) and regional slope terms (cruises 86-1,2 and 86-3) for each of the four 7-d increment widths from 1 wk to 4 wk precapture (Fig. 10). Complete model was: width = constant + SL + region + region × SL.

Cruise	Parameter	Week 1	Week 2	Week 3	Week 4
85-1,2	Region	**	**	—	—
86-1,2	Region × SL	**	**	—	—
86-3	Region × SL	*	*	—	—

age structure of cod between May and June, compared with the change in age structure inshore at region 2i. The hatch date distributions had changed significantly in region 2i during the intervening 3 wk, with the disappearance of older post-larvae (Fig. 7). Thus the spatial distribution of cod in nearshore regions appeared to be more variable, possibly due to poor survival associated with the slower growth rates there or high rates of advection through this region, or both.

Recent Growth Index and Dispersal

The hypothesis that the inshore region of southwestern Nova Scotia was a functional nursery ground for postlarval cod was rejected. The recent growth index in the nearshore habitat was significantly lower than in the offshore for all cruises in both years. This result is surprising given the high concentration of postlarvae seen in this region. If growth is positively correlated with survival (Anderson 1988), then recruitment could be reduced in years when inshore advection predominates (such as in 1985 compared with 1987, Suthers and Frank 1989) — although other factors such as high zooplankton biomass inshore could ameliorate this affect.

FIG. 8. (*continued*)
(Δ), and region 5 (×). The anti-log of SL is shown in parentheses on the abscissa. Shown on the ordinate in parentheses is the increase in SL over 14 d using the otolith radius–SL relationship for each cruise.

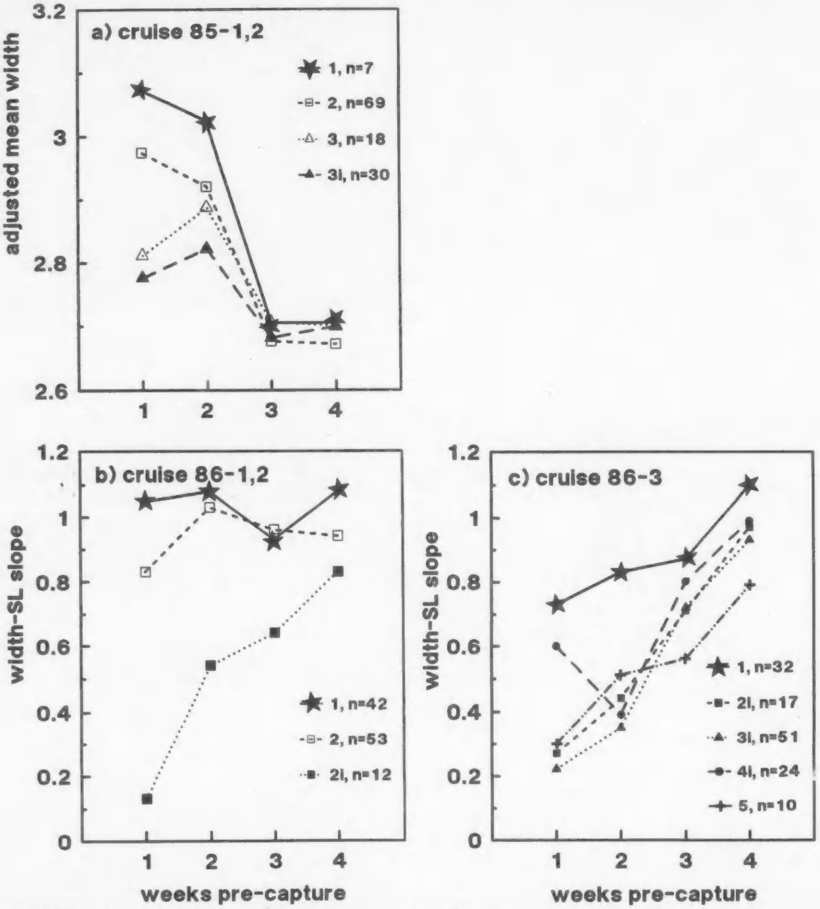

FIG. 10. Regional comparisons of the 7-d increment width–SL regression for weeks 1 to 4 precapture. (a) log mean adjusted widths, cruises 85-1,2 (b) width–SL slopes, cruises 86-1,2 and (c) width–SL slopes, cruise 86-3.

Zooplankton biomass >308 μm was the principal factor that accounted for regional differences in recent growth, assuming that the food and temperature conditions at capture were representative of the previous 14 d. The greatest concentrations of zooplankton occur offshore in the 80–120 m depth range and in the vicinity of Browns Bank (Frank 1988). The gut contents of cod from cruises 85-1,2 largely contained the adult stages of *Calanus finmarchicus* (Budgey 1987). This result is consistent with Marak (1960) who found that the diet of postlarval and pelagic juvenile cod was dominated by copepods, particularly adult *Calanus* (average length 3.5 mm). When the smallest and largest zooplankton size fractions (308–602 and >1050 μm) were included in the multiple regression instead of total zooplankton, there was negligible improvement in the fit of the model. Yet if the analysis was confined to cod >18 mm SL, then the zooplankton size fraction >1050 μm was significantly correlated with the recent growth index ($p<0.03$ for all cruises), while the 308–602 μm size fraction was not ($p>0.1$). Thus not only the abundance but also the size relationship between postlarval cod and their prey can explain variation in increment width and recent growth. Prey abundance and quality have a significant effect on increment width in the laboratory (Volk et al. 1984). Our study presents field evidence of a significant correlation between simultaneous measurements of recent growth and prey abundance of a size suitable for postlarval cod. Similar results using recent otolith growth increment widths, were found in larval Alaskan walleye pollock (*Theragra chalcogramma*) where the highest recent growth over 10 d prior to capture occurred at the station with the greatest zooplankton biomass (Bailey 1989). Current controversies about food availability limiting the growth and survival of larval fish (Anderson 1988; Frank 1988; Sinclair 1988; Taggart and Frank 1989) may largely stem from inappropriate sampling at unsuitable scales. For example length at age is an integrated measure of growth and does not reflect the environmental variables recorded at capture.

Low zooplankton biomass inshore could result from grazing pressure due to high densities of larvae and postlarval fish (up to $6 \cdot m^{-3}$, including sculpins, sandlance, herring, and other blennioids), and of the ctenophore *Pleurobrachia pileus* that can exceed $50 \cdot m^{-3}$ (Milne and Corey 1986). In June 1986, ctenophores were 20–30 fold more abundant inshore than on the Bank, while postlarval fish other than cod were 10–100 fold more abundant (Suthers 1989). At nominal ctenophore densities of $1 \cdot m^{-3}$ the daily consumption of zooplankton would be approximately $4\ mg \cdot m^{-3}$ assuming a ration of $8.5\ mg \cdot d^{-1}$ and a feeding incidence of 50% (Frank 1986). Acknowledging the current uncertainty concerning clearance rates of ctenophores (Miller and Daan 1988; Bell 1988), the daily predation of *Pleurobrachia* alone could equal the inshore standing stock of zooplankton.

Seasonal changes in temperature have been shown to affect otolith increment widths in the field (Campana and Hurley 1989). The equivocal effects shown in this study may be due to the small range in temperature encountered (<3°C range; 85-1,2: 3.5–5.5°C, 86-1,2: 4.0–7.0°C, 86-3: 6.0–8.5°C). Any temperature effect would have been masked by the strong effect of variable feeding conditions that were independent of temperature. Although higher growth rates tended to occur on Browns Bank, water temperature was not always warmer there than inshore.

Growth Indices 4 wk Precapture

The regional differences were more apparent in the most recent 7-d growth index than in the most recent 14-d index. The difference in regional means or width–SL slopes began to diminish before the third week precapture (Fig. 10). This convergence of the growth history suggests a previous mixing of the population between the inshore and offshore, and a common origin on Browns Bank. These growth histories further support the concept that the nearshore cod distributions were not persistent (Fig. 7), but spatially variable at the scale of weeks. The width–SL slopes of region 5 (off Shelburne N.S.) during cruise 86-3 (Fig. 10c) diverged at 3 and 4 wk precapture, suggesting a different origin, perhaps in the northeast (O'Boyle et al. 1984; Campana et al. 1989). Geographical differences have been found in growth histories of fish larvae, corresponding to the local production, and conforming to known subpopulations of adults (Struhsaker and Uchiyama 1976; Nishimura and Yamada 1988). Further analysis of larval growth histories could therefore indicate mixing of larvae of different origin or stocks.

Regional variation in otolith increment widths that was observed is consistent with the findings of other studies that used different techniques to assess the role of food on growth and survival (e.g. O'Connell 1980; Theilacker 1986; Buckley and Lough 1987). For example, Theilacker (1986) found that at stations 350 km offshore in the southern Californian current, nearly 70% of early stage jack-mackeral larvae were starving while only 12% of larvae near coastal banks and islands were starving. These were first feeding larvae, and the geographical differences in condition reflect the stage-specific requirement for copepod nauplii, which were more abundant inshore. The recent growth of cod larvae (<10 mm SL) was not investigated in this study. However, the distributions of larval and postlarval cod off southwestern Nova Scotia were generally coincident (Suthers and Frank 1989); their distributions reflect the influence of the episodic breakdown of the Browns Bank gyre with subsequent transport by the residual circulation. The biomass of large zooplankton (>308 μm) is greatest offshore and on Browns Bank, while landward there is an abundance of smaller (80–153 μm) particles suitable for larvae (Frank 1988). Therefore drift and retention of larval and postlarval cod offshore (>55 m) in southwestern Nova Scotia, would maintain the early life stages of cod in the vicinity of a range of prey sizes. Southwestern Nova Scotia is a highly productive region, through processes such as upwelling (Garrett and Loucks 1976) and a tidal front (Fournier et al. 1984). Distributions of larval herring in eastern Maine (Townsend et al. 1987), and of larval sciaenids in the Gulf of Mexico (Cowan and Shaw 1988) are also coincident with frontal regions. The spawning strategies shown by these fish with regard to dispersal and prey distribution may be quite general and applicable to cod as well.

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References

ANDERSON, J. T. 1988. A review of size dependent survival during prerecruit stages of fishes in relation to recruitment. J. Northw. Atl. Sci. 8: 55–66.

BAILEY, K. M. 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theregra chalcogramma* in the eastern Bering Sea, and cannibalism. Mar. Ecol. Prog. Ser. 53: 205–213.

BELL, K. N. I. 1988. Grazing rates of *Pleurobrachia pileus*. M.Sc. thesis, 124 p. Department of Biology, Dalhousie University, Halifax, N.S.

BOLZ, G. R., AND R. G. LOUGH. 1988. Growth through the first six months of Atlantic cod, *Gadus morhua* and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments. Fish. Bull. 86: 223–235.

BUCKLEY, L. J., AND R. G. LOUGH. 1987. Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44: 14–25.

BUDGEY, H. 1987. The relationship between feeding ecology and dispersal patterns of North Atlantic cod (*Gadus morhua*) larvae in the southwest Nova area. Honours thesis, 35 p. Department of Biology, Dalhousie University, Halifax, N.S.

CAMPANA, S. E. 1987. Image analysis for microscope-based observations: an inexpensive configuration. Can. Tech. Rep. Fish. Aquat. Sci. 1569: iv + 20 p.

CAMPANA, S. E., AND P. C. F. HURLEY. 1989. An age- and temperature mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 46: 603–613.

CAMPANA, S. E., AND J. D. NEILSON. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42: 1014–1032.

CAMPANA, S. E., S. J. SMITH, AND P. C. F. HURLEY. 1989. An age-structured index of cod larval drift and retention in the waters off of southwest Nova Scotia. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 191: 50–62.

CHECKLEY, D. M., S. RAMAN, G. L. MAILLET, AND M. M. MASON. 1988. Winter storm effects on the spawning and larval drift of a pelagic fish. Nature (Lond.) 335: 346–348.

COWAN, J. H., AND R. F. SHAW. 1988. The distribution, abundance, and transport of larval sciaenids collected during winter and early spring from the continental shelf waters off west Louisiana. Fish. Bull. 86: 129–142.

DAAN, N. 1978. Changes in cod stock and cod fisheries in the North Sea. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 172: 39–57.

DOHERTY, P. J., D. MCB. WILLIAMS, AND P. F. SALE. 1985. The adaptive significance of larval dispersal in coral reef fishes. Environ. Biol. Fish. 12: 81–90.

FOURNIER, R. O., M. VAN DET, N. B. HARGREAVES, J. S. WILSON, T. A. CLAIR, AND R. ERNST. 1984. Physical factors controlling summer distribution of chlorophyll *a* off southwestern Nova Scotia. Limnol. Oceanogr. 29: 517–526.

FRANK, K. T. 1986. Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 211–222.

1988. Independent distributions of fish larvae and their prey: natural paradox or sampling artifact? Can. J. Fish. Aquat. Sci. 45: 48–59.

Gagné, J. A., and R. N. O'Boyle. 1984. The timing of cod spawning on the Scotian Shelf, p. 501–517. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flødevigen rapportser 1.

Garrett, C. J., and R. H. Loucks. 1976. Upwelling along the Yarmouth shore of Nova Scotia. J. Fish. Res. Board Can. 33: 116–117.

Gødo, O. R., and K. Sunnanå. 1984. Spawning area and distribution of 0-group cod *Gadus morhua* L., on the Møre coast, p. 519–532. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flødevigen rapportser 1.

Greenberg, D. A. 1983. Modelling the mean barotropic circulation in the Bay of Fundy and Gulf of Maine. J. Phys. Oceanogr. 13: 886–904.

Harden Jones, J. R. 1968. Fish migration. Arnold, London. 325 p.

Hurley, P. C. F., and S. E. Campana. 1989. Distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in waters off southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): (This issue).

Iles, T. D., and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science (Wash., DC) 215: 627–633.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fish. 3: 65–84.

Jones, C. 1986. Determining age of larval fish with the otolith increment technique. Fish. Bull. 84: 91–103.

Lear, W. H., and R. Wells. 1984. Vertebral averages of juvenile cod, *Gadus morhua*, from coastal waters of eastern Newfoundland and Labrador as indicators of stock origin. J. Northw. Atl. Fish. Sci. 5: 23–31.

MacDonald, J. S., M. J. Dadswell, R. G. Appy, G. D. Melvin, and D. A. Methven. 1984. Fishes, fish assemblages, and their seasonal movements in the lower Bay of Fundy and Passamaquoddy Bay, Canada. Fish. Bull. 82: 121–139.

Marak, R. R. 1960. Food habits of larval cod, haddock, and coalfish in the Gulf of Maine and Georges Bank area. J. du Conseil 25: 147–151.

Miller, R. J., and R. Daan. 1989. Planktonic predators and copepod abundance near the Dutch coast. J. Plank. Res. 11: 263–282.

Milne, W. R., and S. Corey. 1986. Distributional patterns of the ctenophores *Pleurobrachia pileus* and *Beroe cucumis* in the Bay of Fundy region, Canada. Can. J. Zool. 64: 2639–2644.

Mosegaard, H., H. Svedang, and K. Taberman. 1988. Uncoupling of somatic and otolith growth rates in arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. 45: 1514–1524.

Neilson, J. D., E. DeBlois, and P. C. F. Hurley. 1988. Stock structure of Scotian Shelf flatfish as inferred from ichthyoplankton survey data and the geographic distribution of mature females. Can. J. Fish. Aquat. Sci. 45: 1674–1685.

Nishimura, A., and J. Yamada. 1988. Geographical differences in early growth of walleye pollock *Theragra chalcogramma*, estimated by back-calculation of otolith daily growth increments. Mar. Biol. 97: 459–465.

Norcross, B. L., and R. F. Shaw. 1984. Oceanic, coastal and estuarine transport of pelagic eggs and larvae with emphasis on fish: a review. Trans. Am. Fish. Soc. 113: 153–165.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 183: 27–40.

O'Connell, C. P. 1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull. 75: 475–489.

Pihl, L. 1982. Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Neth. J. Sea Res. 15: 419–432.

Reznick, D., E. Lindbeck, and H. Bryga. 1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 46: 108–112.

Riley, J. D., and W. G. Parnell. 1984. The distribution of young cod, p. 563–580. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flødevigen rapportser 1.

Secor, D. H., and J. M. Dean. 1989. Somatic growth effects on the otolith–fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46: 113–121.

Sinclair, M. 1988. Marine populations. An essay on population regulation and speciation. Univ. of Washington Press. Seattle. 252 p.

Sinclair, M., and T. D. Iles. 1985. Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine — Scotian Shelf area in relation to oceanographic features. Can. J. Fish. Aquat. Sci. 42: 880–877.

Sinclair, M., and M. J. Tremblay. 1984. Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match–mismatch theory. Can. J. Fish. Aquat. Sci. 41: 1055–1065.

Smith, P. C. 1983. The mean and seasonal circulation off Southwest Nova Scotia. J. Phys. Ocean. 13: 1034–1054.

1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

Struhsaker, P., and J. H. Uchiyama. 1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian islands as indicated by daily growth increments of sagittae. Fish. Bull. 74: 9–17.

Suthers, I. M. 1989. Dispersal and growth of post-larval cod (*Gadus morhua*) off southwestern Nova Scotia. Ph.D. thesis, Dalhousie University, 173 p.

Suthers, I. M., and K. T. Frank. 1989. Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in southwestern Nova Scotia determined with two different gear types. Can. J. Fish. Aquat. Sci. 46: 591–602.

Taggart, C. T., and K. T. Frank. 1989. Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships. American Assoc. Advancement of Science. (In press)

Theilacker, G. H. 1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull. 84: 1–17.

Townsend, D. W., J. P. Christensen, D. K. Stevenson, J. J. Graham, and S. B. Chenoweth. 1987. The importance of a plume of tidally-mixed water to the biological oceanography of the Gulf of Maine. J. Mar. Res. 45: 699–728.

Tremblay, M. J., and M. Sinclair. 1985. Gulf of St. Lawrence cod: age-specific geographic distributions and environmental occurrences from 1971 to 1981. Can. Tech. Rep. Fish. Aquat. Sci. 1387: iv + 43 p.

Volk, E. C, R. C. Wissmar, C. A. Simenstad, and D. M. Eggers. 1984. Relationship between otolith microstructure and the growth of juvenile chum salmon (*Oncorhynchus keta*) under different prey rations. Can. J. Fish. Aquat. Sci. 41: 126–133.

Wilson, K. H., and P. A. Larkin. 1982. Relationship between thickness of daily growth increments in sagittae and change in body weight of sockeye salmon (*Oncorhynchus nerka*) fry. Can. J. Fish. Aquat. Sci. 39: 1335–1339.

Zijlstra, J. J. 1988. Fish migrations between coastal and offshore areas, p. 257–272. *In* B.-O. Jansson [ed.] Coastal–offshore ecosystem interactions. Lecture notes on Coastal and Estuarine Studies, Vol 22. Springer-Verlag, Berlin.

Nutritional Status of Field-Collected Haddock (*Melanogrammus aeglefinus*) Larvae from Southwestern Nova Scotia: An Assessment based on Morphometric and Vertical Distribution Data[1]

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Frank, K. T., and J. K. McRuer. 1989. Nutritional status of field-collected haddock (*Melanogrammus aeglefinus*) larvae from southwestern Nova Scotia: an assessment based on morphometric and vertical distribution data. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): 125–133.

The nutritional status of haddock (*Melanogrammus aeglefinus*) larvae was evaluated during May 1986 over a grid of stations exhibiting variable hydrographic conditions in southwestern Nova Scotia. Over the shallow, well-mixed regions of both the nearshore and western cap of Browns Bank, post-yolk sac haddock larvae exhibited below-average values of Fulton's K ((W/SL^3) × 100, W = weight; SL = standard length) with a correspondingly high proportion of larvae in poor condition (>70%). Conversely, larvae in good condition predominated in the deeper, stratified waters on the eastern cap of the Bank and at off-bank stations to the north along the 100-m isobath. These results agree with published field studies that used either histological or biochemical criteria to evaluate larval condition. Larvae in poor condition also exhibited surface-skewed and frequently bimodal depth profiles in contrast with the unimodal profiles centred at middepth of larvae in good condition, a result consistent with the hypothesis that buoyancy increases in starving larvae. The typically low correlation between larval abundance and recruitment may arise from use of abundance data uncorrected for the proportion of larvae in poor condition. Prorating larval survey data by using proxy variables such as stratification intensity may ultimately increase their predictive utility.

Le statut nutritionnel des larves d'aiglefin (*Melanogrammus aeglefinus*) a été évalué en mai 1986 dans une grille de stations présentant des conditions hydrographiques variables dans le sud-ouest de la Nouvelle-Écosse. Dans les régions peu profondes et bien brassées de l'avant-plage et de la pointe occidentale du banc Browns, les larves d'aiglefin sorties du sac vitellin affichaient des valeurs inférieures à la moyenne pour K de Fulton ((W/SL^3 × 100, W = poids; SL = longueur type) et une proportion correspondante élevée de larves était en mauvais état (>70 %). Par contre, dans les eaux profondes, stratifiées, de la pointe orientale du banc et dans les stations du large du banc jusqu'au nord, le long de l'isobathe de 100 m, les larves en bon état prédominaient. Ces résultats concordent avec ceux des études de terrain publiées qui, à partir de critères histologiques ou biochimiques, évaluaient l'état des larves. Les larves en mauvais état affichaient également des profils de profondeur dissymétriques en surface et souvent bimodaux, contrairement à ceux des larves en bon état, unimodaux et centrés à mi-profondeur, résultat qui concorde avec l'hypothèse selon laquelle la flottabilité des larves affamées augmente. La corrélation typiquement faible entre l'abondance des larves et le recrutement pourrait découler du fait que l'on utilise les données sur l'abondance non corrigées en fonction de la proportion des larves en mauvais état. Le partage au pro-rata des données des dénombrements des larves à l'aide de variables substitutives telles que l'intensité de la stratification pourrait, en dernière instance, en augmenter l'utilité.

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Changes in the adult abundance of marine fish populations may be reflected in larval abundance, but in most cases, recruitment and larval abundance do not appear closely correlated (see reviews in Sissenwine 1984; Fogarty et al. 1987; Peterman et al. 1988). Consequently, the predictive utility of egg and larval surveys has been questioned, except for back-calculation of spawning stock biomass. Recently, it has been argued that the dominant mechanism determining year class strength is predation during the postlarval period and that a shift in the emphasis of field-oriented recruitment studies is required to firmly establish the importance of this phenomenon (Anonymous 1984; Townsend and Cammen 1988). This initiative has been fueled by remarks such as "most field-collected larval fish have a high growth rate and are not on the verge of starvation" (Sissenwine 1984).

The lack of correlation between larval abundance and recruitment rests on the assumption that the survival probability for larvae is the same from year to year. Yet the application of morphometric, histological, and biochemical measurements of field-caught larvae shows that varying proportions were starving and would probably soon die (Table 1). O'Connell (1980) reasoned that since the level of mortality in a population is likely to be a function of the proportion of starving larvae, the proportion could be used to prorate larval abundance estimates.

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[1] Fisheries Ecology Program Contribution Number: 16.

TABLE 1. Recent field studies showing significant variation in larval condition.

Species	Location	Condition index (C.I.)	Variation in C.I. explained by	Reference
Herring	Georges Bank	Morphometric	Location: bank-high, offbank-low	Cohen et al. 1980
Northern anchovy	Southern California Bight	Histological	Plankton displacement volume	O'Connell 1980
Pacific herring	Departure Bay, B.C.	W/L^b	Not evaluated	Westernhagen and Rosenthal 1981
P. gunnellus	Gulf of Maine	W/L^b	Copepod nauplii	Townsend 1983
Cod	Gulf of Maine	W/L^b	Copepod nauplii	Koslow et al. 1985
Silver hake	Scotian Shelf	Morphometric	Total zooplankton	Noskov et al. 1985
Jack mackerel	Southern California Bight	Histological, morphometric	Location: offshore-poor, island/bank-good	Theilacker 1986
Cod, haddock	Georges Bank	RNA:DNA	Copepod nauplii, copepodites Stratification intensity	Buckley and Lough 1987
Striped bass	Potomac and Choptank River estuary	Morphometric, RNA:DNA, lipid class analysis, histological	Not evaluated	Setzler-Hamilton et al. 1987
Northern anchovy	Southern California Bight	Lipid class analysis	Copepod triacylglycerol	Hakanson 1989

Such an adjustment should yield a better estimate of ultimate year class success if based on adequate sampling. There are some compelling reasons to believe that this is so. For example, sublethal effects in response to environmental variation induced at one stage of development are usually expressed in a later stage of development in terms of reduced survival potential (Rosenthal and Alderdice 1976; Martin and Wright 1987), and size differences expressed during the larval period persist well into the juvenile period (Rosenberg and Haugen 1982; Chambers et al. 1988).

The first step towards prorating larval abundance estimates is to establish a link from the larvae to the causal factor and eventually to a proxy variable. Several of the studies listed in Table 1 show that food availability is directly related to the criteria chosen for evaluating larval condition. In addition, the results of several studies have shown that the mixing regime exerts a strong effect on food availability for larvae on either event/seasonal time scales (Lasker 1975; Lough 1984; Tilseth and Ellertsen 1984; Ellertsen et al. 1984; Peterson and Ausubel 1984) or from site to site within the distributional range (Lough 1984; Buckley and Lough 1987). Mixing apparently disperses the high concentrations of prey necessary for successful feeding. Several laboratory studies have shown that the specific gravity of larvae decreased (or buoyancy increased) with starvation due to the combined effect of increased water content and decreased protein in the tissues (herring, plaice: Blaxter and Ehrlich 1974; Yin and Blaxter 1987; cod: Tilseth and Stromme 1976; Neilson et al. 1986; Yin and Blaxter 1987; flounder: Yin and Blaxter 1987). The collective results of these published studies are shown in Fig. 1 which provided a research framework for the study reported here.

In this paper we describe geographic patterns in the condition of haddock (*Melanogrammus aeglefinus*) larvae off southwestern Nova Scotia and evaluate the relationship between larval condition and the prevailing mixing/stratification regime. The prediction was that haddock larvae would be in relatively poor condition at well-mixed sites and in good condition at stratified sites in the survey area. In essence this objective is an expanded test of a hypothesis developed by Buckley and Lough (1987) from RNA:DNA-based condition data for haddock larvae collected at three sites on Georges Bank. We utilized a morphometric based condition index which was applied to haddock larvae collected over a much broader geographic area. We also evaluated interstation variability in the vertical distribution of haddock larvae in order to assess whether or not the buoyancy changes associated with starving larvae in laboratory studies would be expressed in field collections.

Materials and Methods

Haddock larvae were obtained from collections made at 34 stations distributed over the nearshore and offshore waters of southwestern Nova Scotia during 9–20 May 1986. The southernmost stations were located over Browns Bank, a major spawning ground for haddock during April–May (O'Boyle et al. 1984), and the northerly stations included the nearshore waters (<60 km from shore) off Nova Scotia. We expected to encounter a wide range of hydrographic conditions within the survey area based on previous studies of the physical oceanography in the region (Smith 1983, 1989).

We used a half-scale version of the BIONESS (Sameoto et al. 1980) at each station to obtain discrete depth collections of haddock larvae. At each station the net was lowered to the maximum sampling depth and samples were obtained sequentially at 55, 45, 35, 20, 10, and 5 m. Each depth was sampled for 7–8 min at towing speeds averaging 1.5 m/s. The mouth area of each of the seven 333-μm-mesh nets was 0.25 m^2. A CTD positioned on top of the net frame provided real-time measurements of temperature, salinity, and depth. Further details of the sampling gear are available in Frank (1988). BIONESS sampling was conducted on a 24-h basis and ceased only under inclement weather conditions.

All samples were preserved in 4% formalin buffered with sodium borate. Haddock larvae were removed from each sample and measured to the nearest 0.01 mm with the aid of a binocular dissection microscope fitted with a calibrated ocular micrometer. Standard length and anal body depth were determined and we also noted the state of each larva with respect to the presence or absence of a yolk sac and missing body parts (eyes, gut, etc.). No correction was made for shrinkage as Bolz and Lough (1983) had done for haddock larvae on Georges Bank. They used an algorithm devised for shrinkage of larval northern anchovy (*Engraulis mordax*) (Theilacker 1980). Because of the narrow range of sizes of haddock larvae present in our collections and the lack of a relationship between preserved and fresh standard length for haddock, we did not apply

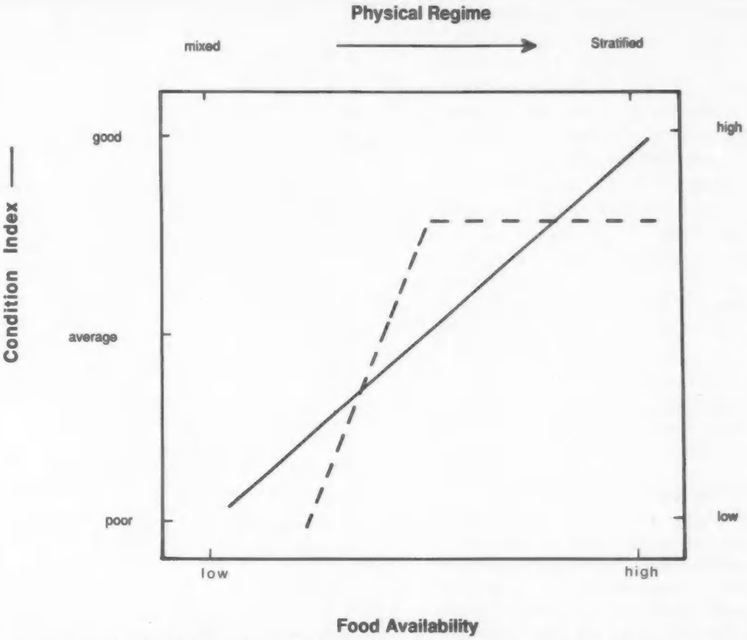

FIG. 1. Composite model of expected changes in body condition (—) and buoyancy (- - -) of post-yolk sac fish larvae in relation to food availability and stratification intensity. Not shown is the time course of change associated with moribund larvae: their specific gravity increases, osmoregulation fails, and they become negatively buoyant as they die (Blaxter and Ehrlich 1974).

a length correction algorithm. Weights of larvae were obtained by drying individual larvae in preweighed aluminum pans at 60°C for 24 h, removing them to a desiccator, and weighing to an accuracy of 1 μg. Only larvae undamaged by net collection and without yolk sacs were evaluated. This is in direct contrast with a recent study that included all larvae in weight determinations and that was critical of the use of dry weights as an index of larval condition (McGurk 1985).

Regression analysis of the logarithmic transformed weight (W) and standard length (SL) of haddock larvae provided an estimate of the exponent b for the condition index chosen for analysis, i.e. the relative condition factor $(W/\mathrm{SL}^b) \times 100$. The suitability of this index to provide an unbiased estimate of larval condition was examined by testing for covariation with standard length, time of day, and tow duration.

Variation in the vertical distribution of haddock larvae in relation to the mean condition of larvae at each station was evaluated by calculating the depth of the centre of mass of the distribution, Z_{cm} (metres):

$$Z_{\mathrm{cm}} = \sum_{i=1}^{7} (p_i Z_i)$$

where p_i is the proportion of larvae in the ith depth interval and Z_i is the depth of the ith stratum.

Results

Morphometric Condition Factor

The average length, dry weight, and numerical density of haddock larvae collected during the May 1986 survey were 6.1 mm (range 2.9–12.4), 149 μg (range 20–1386), and 10 larvae/100 m^3 (range of means among stations 0–117), respectively. The majority of larvae (66%) collected relative to the total in the survey area were distributed in the vicinity of Browns Bank (Frank et al. 1989).

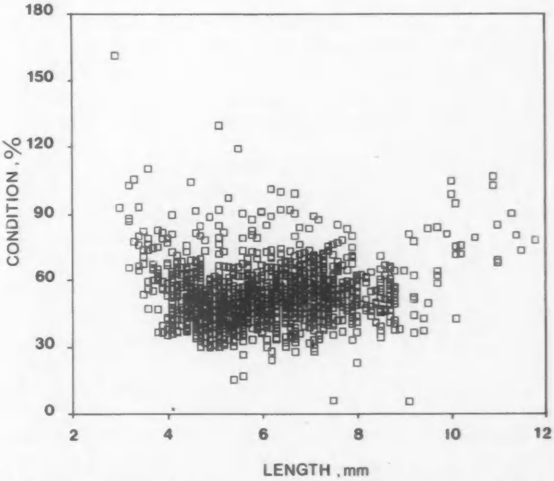

FIG. 2. Relationship between condition as determined from Fulton's K $((W/\mathrm{SL}^3) \times 100)$ and standard length for haddock larvae collected during May 1986.

The relationship between dry weight and standard length was described by the equation

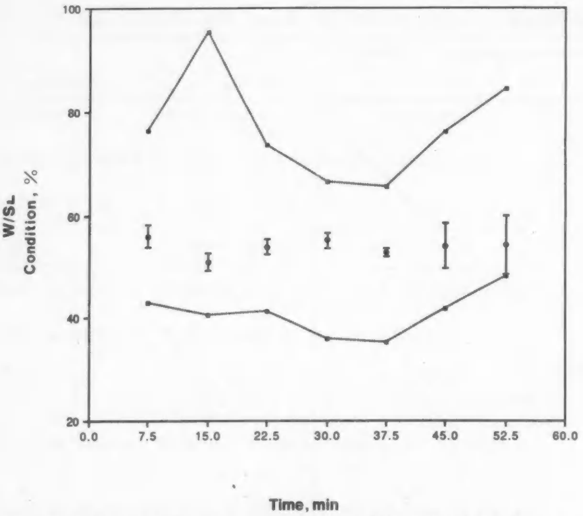

FIG. 3. Relationship between percentage condition of haddock larvae averaged over all stations by towing depth and time since capture from BIONESS collections. The first depth stratum sampled was always the deepest one, and therefore, haddock larvae at this level experienced the longest prepreservation time (52.5 min). Error bars show 95% confidence interval and connected lines show maximum and minimum K values.

$$W = 0.495 \times SL^{3.029}, \qquad R^2 = 0.88, n = 1234, \quad p < 0.0001.$$

Given this result, we chose to use Fulton's K (W/SL^3) (LeCren 1951) as an index of condition due to the closeness of the empirically derived exponent b to 3 and its widespread use in other published studies. A possible source of bias associated with the use of this index is covariation with standard length, while in general both tow duration and time of day could exert a confounding effect.

Fulton's K was independent of standard length ($r = 0.07$, $n = 1234$), showing roughly equal variation about a grand mean of 53% over the entire range of haddock lengths examined (Fig. 2). This result was nearly identical to a similar analysis using the empirically derived exponent ($b = 3.029$). The average value of Fulton's K at each sampling depth was independent of time since capture ($r = 0.01$, $n = 7$, $p > 0.05$) which ranged from 52.5 min for samples obtained at the maximum sampling depth to 7.5 min for samples collected at 5 m with the BIONESS (Fig. 3). Fulton's K did exhibit a peak positive relationship with time of day ($r = 0.2$, $n = 1234$) although the predicted range of variation in condition between day and night was less than 0.2%. We did not, therefore, make any adjustments for time of day in the analysis of variation in larval condition. Collectively, these results indicate that Fulton's K for haddock larvae collected during May in southwestern Nova Scotia is an unbiased indicator of condition.

Physical Regime

Well-mixed sites in the survey area generally coincided with those stations located in shallow waters on the western cap of Browns Bank and to the north in the nearshore waters off Cape Sable and German Bank (Fig. 4). Mixed conditions at these sites reflected the influence of tides, and these locations tend to remain mixed year round. All other stations within the survey area, principally in the offshore regions, were stratified to varying degrees (Fig. 4). Our description of the physical environment is entirely consistent with previous studies by Garrett et al. (1978), Fournier et al. (1984), and Smith (1983, 1989).

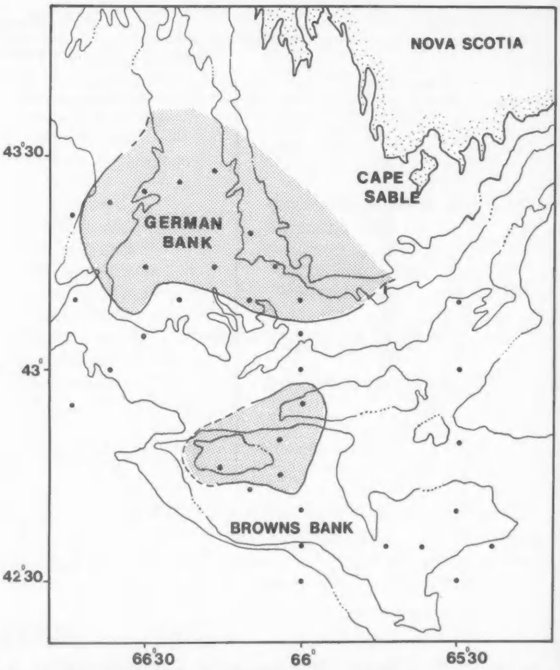

FIG. 4. Southwestern Nova Scotia showing locations of well-mixed regions (stippled) in the survey area. Well-mixed areas were defined as such when $((\Delta \text{ sigma-}t/\Delta Z) \times 1000) < 8$. All other areas exhibited varying degrees of stratification intensity. ●, sampling stations. Z refers to the maximum sampling depth.

Mixing/Stratification Effects on Condition

Haddock larvae were in relatively poor condition at well-mixed sites and in good condition at stratified sites (Fig. 5), which is consistent with our prediction (see the introduction). Haddock condition was below average in the well-mixed regions depicted in Fig. 4. Conversely, haddock larvae exhibited above-average condition in the stratified, offshore areas to the north of Browns Bank and at the deepwater stations on the eastern cap of the Bank (Fig. 5). Similar patterns were apparent when we examined the proportion of larvae at a given station, with a value of Fulton's K in excess of the grand mean. In the two well-mixed regions this value ranged from 10 to 41% (mean 29%; 95% C.I. 18–41%) in the nearshore and from 30 to 38% (mean 33%; 95% C.I. 25–42) in the offshore western cap of the Bank. In marked contrast with the mixed sites, the proportion of larvae in good condition ranged from 44 to 78% (mean 60%; 95% C.I. 53–68%) within the stratified sites.

There was a weak positive correlation ($r = 0.44$, $n = 19$, $p < 0.06$) between the average condition of haddock larvae (by station) and stratification intensity (defined as (sigma-t at maximum sampling depth — sigma-t at 5 m)/(maximum sampling depth − 5 m) × 1000) over the survey area. However, the percentage of larvae in good condition (Y) was significantly related to stratification intensity (X):

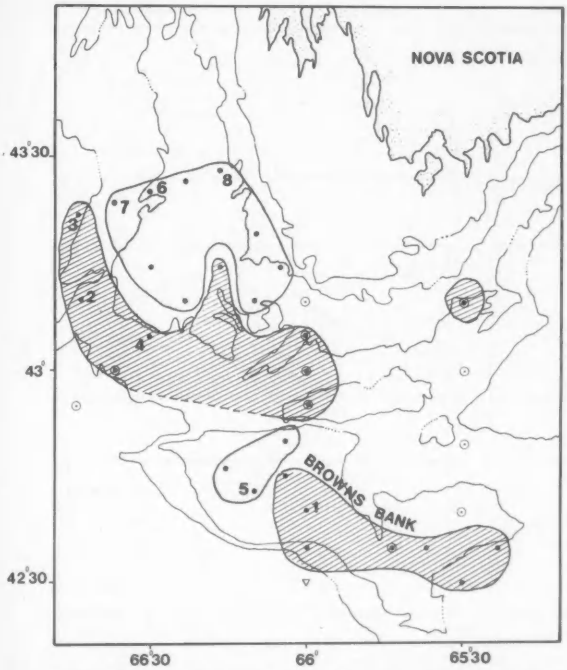

FIG. 5. Distribution of haddock larvae whose mean condition (K) per station was above (diagonal lines) or below (stippling) the grand mean over the survey area. ⊙, no larvae available for dry weight; ∇, gear malfunction; ◉, low n (< 9 larvae per station). On average, 63 larvae per station (range 9–183) were used to evaluate the condition of haddock larvae on a station-by-station basis over the survey area.

$$Y = 20.1 + 2.91X, \qquad r = 0.55, n = 19, p < 0.05.$$

The percentage of larvae in good condition was strongly positively correlated with the average condition of larvae from station to station within the survey area ($r = 0.89$, $p < 0.001$). It is interesting to note that the densities of haddock larvae over the shallow, well-mixed western cap of Browns Bank were up to 10-fold greater than the survey mean (Frank et al. 1989). Steep topographic gradients in combination with strong semidiurnal tides in this region produce a gyral circulation (Smith 1989) that could retain larvae for varying amounts of time and thus account for the high densities there. Relatively high densities of haddock larvae have been noted in this region during several previous surveys (Campana et al. 1989).

Buoyancy Changes and Starving Larvae

Previous analysis of the vertical distribution of haddock larvae has shown no evidence of differences between day and night depth distributions with the average centre of mass occurring at a depth of 29 m (Frank et al. 1989). The occurrence of haddock larvae at middepth appears to persist well into the postlarval period (Miller et al. 1963; Perry and Neilson 1988). This feature of the early life history of haddock simplifies the analysis of the depth distribution in relation to their condition.

We expected that haddock larvae in poor condition would be relatively more buoyant than larvae in good condition and that such differences would be evident in their depth profiles. The first step in this analysis was to examine depth profiles from several of the stations where haddock larvae were in above- and below-average condition. The depth profiles of discrete (1 mm) size groups of haddock larvae from 4 to 7 mm that were in above-average condition exhibited a unimodal peak at middepth centred about 30 m (Fig. 6). This situation was also evident when all sizes of haddock larvae were combined. In striking contrast were the depth profiles of below-average condition larvae that were both surface skewed and frequently bimodal (Fig. 7). Furthermore, Z_{cm} decreased with size of the larvae ($r = 0.76$, $p < 0.01$), ranging from a predicted Z_{cm} of 25 m at a size of 4 mm to 12 m at 7 mm (Fig. 8). No such size-dependent trend was evident among larvae in above-average condition ($r = 0.05$, $p > 0.05$); rather, the Z_{cm} of each 1-mm size interval was centred about a mean of 29 m (Fig. 8). Collectively, these results support the prediction that poor-condition larvae experience an increase in buoyancy.

The second step in this analysis involved estimating the water density (sigma-t) occurring at Z_{cm} of haddock larvae (all sizes) at each station. We observed a progressive increase in sigma-t as a function of the mean condition of larvae (Fig. 9):

$$\text{Sigma-}t = 24.12 + 0.0219 \times \text{Fulton's } K, \qquad r = 0.61, p < 0.001.$$

The existence of such a relationship provides the first field demonstration of the laboratory result that buoyancy increases (or specific gravity decreases) as larvae starve.

Discussion

Our study revealed that the condition of haddock larvae was strongly influenced by the local mixing/stratification regime, a result consistent with the findings of Buckley and Lough (1987) for haddock larvae on Georges Bank, and that variation in the depth distribution of the larvae was consistent with the laboratory-generated hypothesis that starving larvae become increasingly buoyant. The occurrence of larvae in below-average condition was not typified by isolated cases at widely scattered locations; instead, patches were seen over several contiguous stations in the shallow nearshore waters off southwestern Nova Scotia and the western cap of Browns Bank (Fig. 4 and 5). This increased our confidence that the criterion chosen to evaluate the nutritional status of haddock larvae was appropriate and capable of resolving spatial patterns in the distribution of starving larvae.

The similarity of our findings to those of Buckley and Lough (1987) who used biochemical methods of analysis also suggests that morphometric based condition indices can provide a meaningful assessment of larval haddock condition. This suggestion is contrary to the arguments advanced by McGurk (1985) for rejecting the general use of such indices and Fulton's K in particular. McGurk (1985) made the following criticisms: Fulton's K is correlated with standard length; the assumption of isometry ($b = 3$) is incorrect because the weight–length exponent of larval fishes is closer to 4 (Laurence (1979) was cited in support of this claim); and Fulton's K does not include information on nutritional status contained in other body dimensions such as anal body depth, head width, eye diameter, etc. We do not accept these criticisms. No correlation was evident between Fulton's K and standard length (Fig. 2), and assuming the most appropriate statistical model is fitted to the data, patterned residual variation should be minimal. We showed that $b = 3.03$, and other workers have obtained similar values. For example, Economou (1987) showed that the larvae of five gadoid species

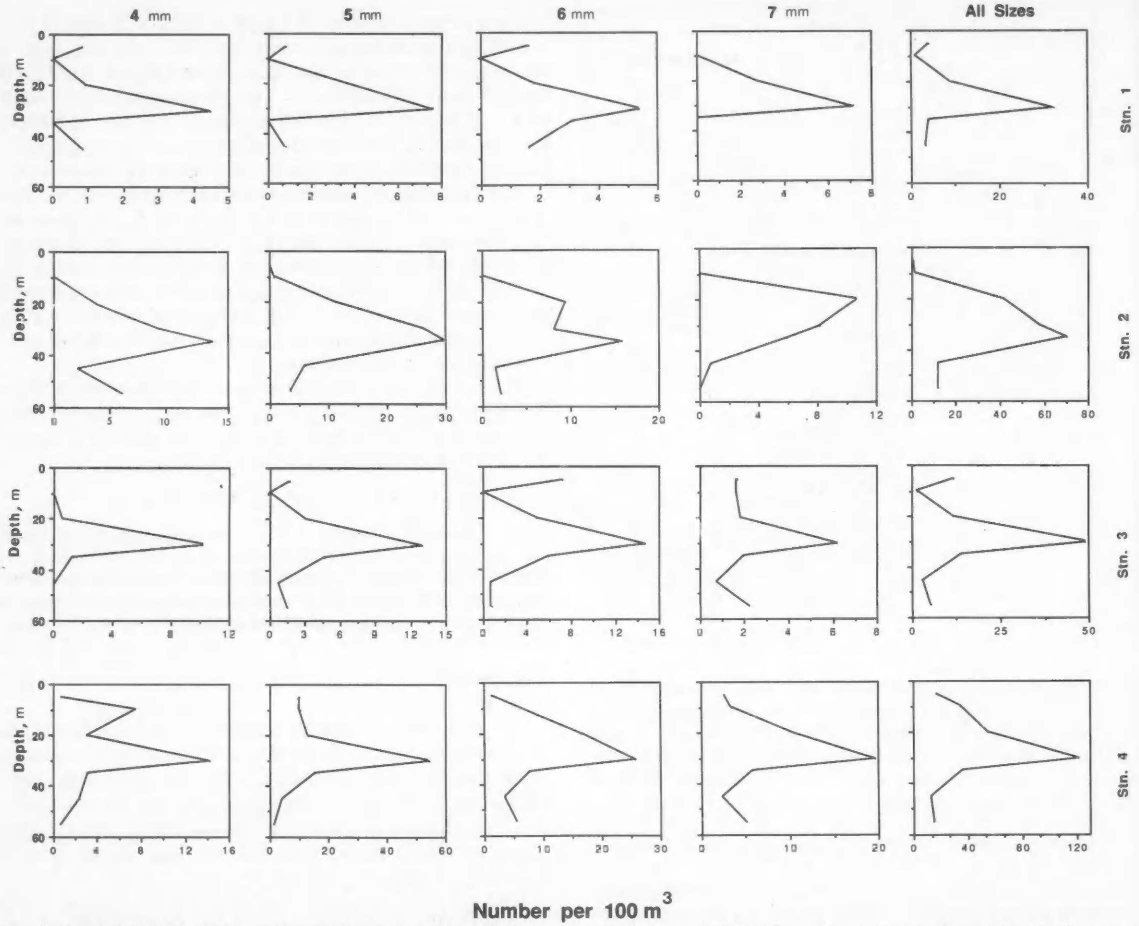

FIG. 6. Depth distribution of four discrete size groups of haddock larvae and all sizes combined from four representative stations in the survey area where the mean condition (*K*) was above average. Stations 1–3 were sampled during the daytime (range 1350–1920) and station 4 was sampled at nighttime (0220). See Fig. 5 for station locations.

collected in the northern North Sea exhibited *b*'s ranging from 2.92 to 3.22. Furthermore, the analysis of weight–length relationships by Laurence (1979) was based on larvae obtained from experimental spawning of adults and subsequently reared in the laboratory. The growth patterns of laboratory-reared larvae are often very different from those in the field (Balbontin et al. 1973; Blaxter 1976) which can render laboratory calibrations and their associated parameters of uncertain pertinence to field conditions. At any given length, laboratory-reared plaice and herring larvae were heavier by as much as 30% compared with those from wild populations (Blaxter 1976). In our study, anal body depth was highly correlated with dry weight ($r = 0.92$, $n = 1234$), and previous studies have shown that discrete indices of relative condition are correlated, showing equal sensitivity to environmental conditions (Koslow et al. 1985; Theilacker 1986; Setzler-Hamilton et al. 1987). In addition, there does not appear to be any advantage in performing multivariate analyses based on several morphological measurements (Koslow et al. 1985).

To our knowledge the study reported here represents the first field verification of the laboratory result that larvae become increasingly buoyant with starvation (Neilson et al. 1986). Changes in the depth distribution of starving haddock larvae presumably resulted from the catabolism of protein in the tissue and replacement by water which generates lift (Blaxter and Ehrlich 1974). Contrary to our results the depth distributions of good- and poor-condition haddock larvae on Georges Bank did not vary appreciably between three sampling sites, one mixed and two stratified (Buckley and Lough 1987). The lack of variation in the depth distribution could have been due to the superior discriminating power of the method used by Buckley and Lough (1987) to assess gradations of larval condition (i.e. RNA:DNA analysis) relative to the coarseness of Fulton's *K* (our study). It is also possible that because they sampled just one station on Georges Bank where mixing conditions prevailed, it limited the opportunity for observing variation in larval depth distributions. Nevertheless, *our* results suggest that variation in the depth distribution of larvae provides a means of diagnosing the proportion of starving larvae in a population. Care must be taken not to incorrectly ascribe such depth variation to either time of day, sampling error, or ontogenetic events (e.g. Fig. 8) during the early life history.

Stratification intensity was a better predictor of larval condition, in terms of both the average condition and the percent-

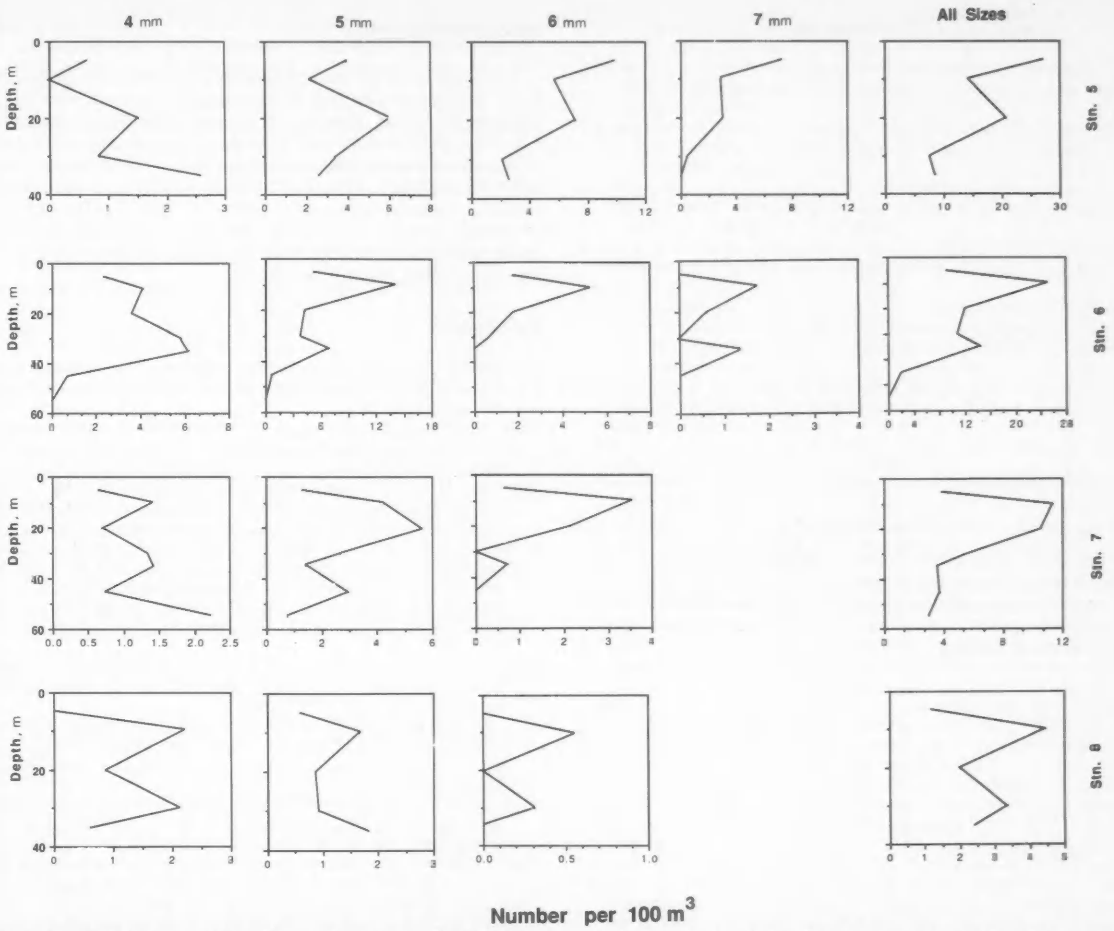

FIG. 7. Depth distribution of four discrete size groups of haddock larvae and all sizes combined from four representative stations in the survey area where the mean condition (K) was below average. Stations 1–3 were sampled during the daytime (range 0705–1050) and station 4 was sampled at nighttime (0230). See Fig. 5 for station locations.

age of larvae in good condition, than any other variable examined including food abundance ($r < -0.42$, $p > 0.05$). Relatively low food levels generally typify all of the bank stations (Frank 1988), yet broad patches of poor- and good-condition larvae were found on the eastern and western cap, respectively (Fig. 5). As we have shown, the major difference between these areas was in their mixing characteristics (Fig. 4). Also, higher food levels are a general characteristic of the nearshore (Frank 1988) where most larvae were in poor condition during May 1986. These results are at odds with the description of the feeding conditions for haddock larvae on Georges Bank. At the stratified sites, food levels were at least an order of magnitude greater than at the mixed site and the larval population centres coincided with prey biomass vertically (Buckley and Lough 1987). In our May 1986 survey, prey biomass was generally unrelated to stratification intensity. However, discrete depth estimates of prey biomass were not available because the mesh size of the BIONESS nets was too large to retain the preferred prey sizes (100 – 450 μm) for haddock larvae (Kane 1984). Instead, depth-integrated vertical hauls of an 80-μm-mesh net were used to collect microzooplankton. Unfortunately, this collection technique is incapable of resolving any subsurface maximum in prey abundance which probably accounts for the discrepancy between our results and those of Buckley and Lough (1987). Furthermore, the average prey biomass in southwestern Nova Scotia during May 1986 was four- to sixfold lower than in previous years (Frank 1988) which could have accentuated the effect of stratification intensity on food availability for haddock larvae.

The ecological implications of starvation-induced changes in depth distribution through increased buoyancy are many. Not only does starvation diminish the tolerance of larvae to certain environmental factors (Yin and Blaxter 1987), but due to the changing depth distribution it can put the larvae at risk to a suite of anomalous physical and biological conditions. For example, surface currents driven by wind could transport larvae into areas outside the normal distributional range. Increased predation resulting from residence in the well-lit surface waters is another possibility suggested by Neilson et al. (1986). In this sense, starvation, through its influence on the buoyancy characteristics of marine fish larvae, exacerbates the negative effects of some environmental factors. Laboratory concepts such as the point-

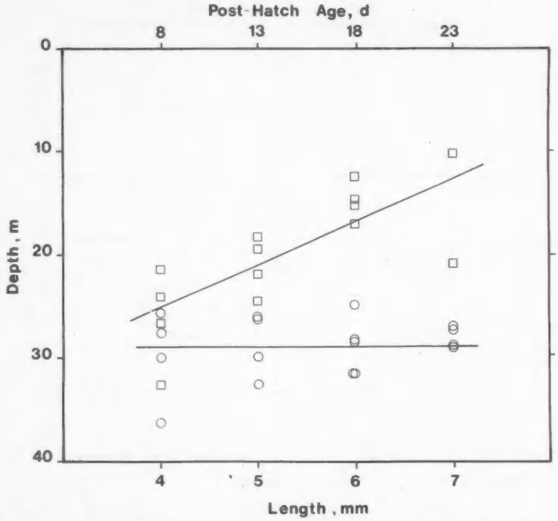

FIG. 8. Depth of the centre of mass of discrete size groups of haddock larvae from stations where the mean condition (*K*) was above (○) or below (□) average. Data for this analysis were taken from Fig. 6 and 7. Ages were approximate and based on published estimates of growth rate and size at hatching.

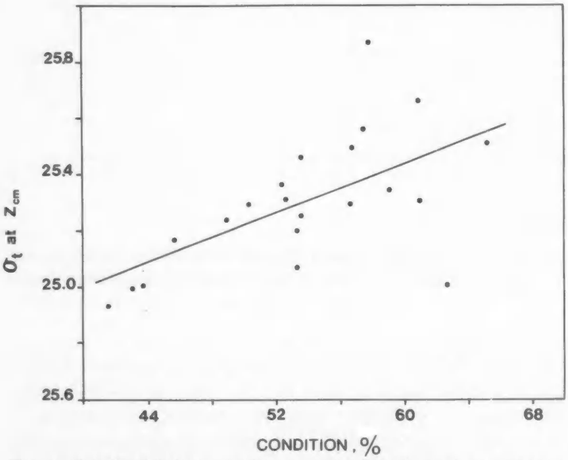

FIG. 9. Relationship between the water density (sigma-*t*) occurring at the depth of the centre of mass of haddock larvae and the corresponding mean condition (*K*) of larvae from station to station within the survey area.

of-no-return (Blaxter and Hempel 1963) might have limited application in field situations, given the suite of detrimental events associated with starving larvae. It is not unreasonable to expect that once a larva reaches a poor condition it will remain that way. The possibility that future survival is established during the early larval stage underlies our belief that prorating larval abundance data for larval condition will yield better predictive capabilities of recruitment than unadjusted abundance data. Finally, the high densities of haddock larvae in poor condition that were evident on the shallow western cap of Browns Bank reinforce our view that abundance data alone do not provide an adequate measure of potential year class strength.

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References

ANONYMOUS. 1984. Issue paper. Redirection of NEFC recruitment studies. NOAA, National Marine Fisheries Service, Northeast Fishery Center, Narragansett, RI. 20 p.

BALBONTIN, F., S. S. DESILVA, AND K. F. EHRLICH. 1973. A comparative study of anatomical and chemical characteristics of reared and wild herring. Aquaculture 2: 217–240.

BLAXTER, J. H. S. 1976. Reared and wild fish-how do they compare?, p. 11–26. *In* G. Persoone and E. Jaspers [ed.] Proceedings of the 10th European symposium on marine biology. Universa Press, Wetteren, Belgium.

BLAXTER, J. H. S., AND K. F. EHRLICH. 1974. Changes in behaviour during starvation of herring and plaice larvae, p. 575–588. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York, NY.

BLAXTER, J. H. S., AND G. HEMPEL. 1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Perm. Int. Explor. Mer 28: 211–240.

BOLZ, G. R., AND R. G. LOUGH. 1983. Growth of larval Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, on Georges Bank, spring 1981. Fish. Bull. 81: 827–836.

BUCKLEY, L. J., AND R. G. LOUGH. 1987. Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44: 14–25.

CAMPANA, S. E., S. J. SMITH, AND P. C. F. HURLEY. 1989. A drift–retention dichotomy for larval haddock (*Melanogrammus aeglefinus*) spawned on Browns Bank. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): (This issue).

CHAMBERS, R. C., W. C. LEGGETT, AND J. A. BROWN. 1988. Variation in and among early life history traits of laboratory-reared winter flounder *Pseudopleuronectes americanus*. Mar. Ecol. Prog. Ser. 47: 1–15.

COHEN, R. E., R. G. LOUGH, AND J. A. MURPHY. 1980. Larval herring (*Clupea harengus* L.) gut content and morphological condition data from three spawning seasons (1974, 1975, and 1976) in the Georges Bank – Gulf of Maine area. NAFO SCR Doc. 80/IX/134: 13 p.

ECONOMOU, A. N. 1987. Ecology of survival in some gadoid larvae of the northern North Sea. Environ. Biol. Fishes 4: 241–260.

ELLERTSEN, B., P. FOSSUM, P. SOLEMDAL, S. SUNDBY, AND S. TILSETH. 1984. A case study of the distribution of cod larvae and availability of prey organisms in relation to physical processes in Lofoten. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flodevigen Rapportser 1 (1984): 453–477.

FOGARTY, M. J., M. P. SISSENWINE, AND M. D. GROSSLEIN. 1987. Fish population dynamics, p. 494–507. *In* R. H. Backus [ed.] Georges Bank. MIT Press, Cambridge, MA.

FOURNIER, R. O., M. VAN DET, N. B. HARGREAVES, J. S. WILSON, T. A. CLAIR, AND R. ERNST. 1984. Physical factors controlling summer distribution of chlorophyll *a* off southwestern Nova Scotia. Limnol. Oceanogr. 29: 517–526.

FRANK, K. T. 1988. Independent distributions of fish larvae and their prey: natural paradox or sampling artifact? Can. J. Fish. Aquat. Sci. 45: 48–59.

FRANK, K. T., F. H. PAGE, AND J. K. MCRUER. 1989. Hydrographic effects on the vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae on the southwestern Scotian Shelf. Can. J. Fish. Aquat. Sci. 46(Suppl. 1): (This issue).

GARRETT, C. J. R., J. R. KEELEY, AND D. A. GREENBERG. 1978. Tidal mixing versus thermal stratification in the Bay of Fundy and Gulf of Maine. Atmosphere-Ocean 16: 403–423.

HAKANSON, J. L. 1989. Condition of larval anchovy (*Engraulis mordax*) in the southern California Bight, as measured through lipid analysis. Mar. Biol. 102: 53–159.

KANE, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Mar. Ecol. Prog. Ser. 16: 9–20.

Koslow, J. A., S. Brault, J. Dugas, R. O. Fournier, and P. Hughes. 1985. Condition of larval cod (*Gadus morhua*) off southwest Nova Scotia in 1983 in relation to plankton abundance and temperature. Mar. Biol. 86: 113–121.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. 73: 453–462.

Laurence, G. C. 1979. Larval length–weight relations for seven species of northwest Atlantic fishes reared in the laboratory. Fish. Bull. 76: 890–895.

LeCren, E. D. 1951. The length–weight relationship and seasonal cycle on gonad weight and condition in perch (*Perca fluviatilis*). J. Anim. Ecol. 20: 201–219.

Lough, R. G. 1984. Larval fish trophodynamic studies on Georges Bank: sampling strategy and initial results. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flodevigen Rapportser 1 (1984): 395–434.

Martin, F. D., and D. A. Wright. 1987. Nutritional state analysis and its use in predicting striped bass recruitment: laboratory calibration. Am. Fish. Soc. Symp. 2: 109–114.

McGurk, M. D. 1985. Effects of net capture on the postpreservation morphometry, dry weight, and condition factor of Pacific herring larvae. Trans. Am. Fish. Soc. 114: 348–355.

Miller, D., J. B. Colton, and R. R. Marak. 1963. A study of the vertical distribution of larval haddock. J. Cons. Int. Explor. Mer 178: 144–149.

Neilson, J. D., R. I. Perry, P. Valerio, and K. G. Waiwood. 1986. Condition of Atlantic cod *Gadus morhua* larvae after the transition to exogenous feeding: morphometrics, buoyancy and predator avoidance. Mar. Ecol. Prog. Ser. 32: 229–235.

Noskov, A. S., A. I. Sherstjukov, and V. I. Vinogradov. 1985. Distribution and fluctuations of the Scotian silver hake abundance in early stages. NAFO SCR Doc. 85/114: 16 p.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 183: 27–40.

O'Connell, C. P. 1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull. 78: 475–489.

Perry, R. I., and J. D. Neilson. 1988. Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. Mar. Ecol. Prog. Ser. 49: 199–214.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45: 8–16.

Peterson, W. T., and S. J. Ausubel. 1984. Diets and selective feeding by larvae of Atlantic mackerel *Scomber scombrus* on zooplankton. Mar. Ecol. Prog. Ser. 17: 65–75.

Rosenberg, A. A., and A. S. Haugen. 1982. Individual growth and size-selective mortality of larval turbot (*Scophthalmus maximus*) reared in enclosures. Mar. Biol. 72: 73–77.

Rosenthal, H., and D. F. Alderdice. 1976. Sublethal effects of environmental stressors, natural and pollutional, on marine fish eggs and larvae. J. Fish. Res. Board Can. 33: 2047–2065.

Sameoto, D. D., L. O. Jaroszynski, and W. B. Fraser. 1980. BIONESS, a new design in multiple net zooplankton samplers. Can. J. Fish. Aquat. Sci. 37: 722–724.

Setzler-Hamilton, E. M., D. A. Wright, F. D. Martin, C. V. Millsaps, and S. I. Whitlow. 1987. Analysis of nutritional condition and its use in predicting striped bass recruitment: field studies. Am. Fish. Soc. Symp. 2: 115–128.

Sissenwine, M. P. 1984. Why do fish populations vary?, p. 59–94. *In* R. M. May [ed.] Exploitation of marine communities. Dahlem Konferenzen 1984. Springer-Verlag, Berlin.

Smith, P. C. 1983. The mean and seasonal circulation off southwest Nova Scotia. J. Phys. Oceanogr. 13: 1034–1054.

1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

Theilacker, G. H. 1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull. 78: 685–692.

1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull. 84: 1–17.

Tilseth, S., and B. Ellertsen. 1984. The detection and distribution of larval Arcto–Norwegian cod, *Gadus morhua*, food organisms by an in situ particle counter. Fish. Bull. 82: 141–156.

Tilseth, S., and T. Stromme. 1976. Changes in buoyancy and activity during starvation of cod larvae (*Gadus morhua* L.). ICES CM 1976/F:33: 12 p.

Townsend, D. W. 1983. The relations between larval fishes and zooplankton in two inshore areas of the Gulf of Maine. J. Plankton Res. 5: 145–173.

Townsend, D. W., and L. M. Cammen. 1988. Potential importance of the timing of spring plankton blooms to benthic–pelagic coupling and recruitment of juvenile demersal fishes. Biol. Oceanogr. 5: 215–229.

Westernhagen, H.V., and H. Rosenthal. 1981. On condition factor measurements in Pacific herring larvae. Helgol. Meeresunters. 34: 257–262.

Yin, M. C., and J. H. S. Blaxter. 1987. Temperature, salinity tolerance, and buoyancy during early development and starvation of Clyde and North Sea herring, cod, and flounder larvae. J. Exp. Mar. Biol. Ecol. 105: 73–83.

Demersal Fish Assemblages on the Scotian Shelf, Northwest Atlantic: Spatial Distribution and Persistence[1]

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This study is based on 18 surveys, 12 in summer, and three each in spring and fall, with bottom trawls over the Scotian Shelf and Bay of Fundy. The data analysis sequence was: temporal and spatial aggregation of trawl sets; estimation of interspecies and intersite distance indices; clustering and ordination of sites and species, and discrimination of site groups using environmental variables. Nine species-groups, and 10 site-groups were defined, and displayed in a two-way table. Depth and temperature were the environmental variables most strongly associated with differences in assemblage structure among site-groups. Changes in assemblage structure from one area to another were distinct but apparently gradual, with no sharp assemblage boundaries. This pattern is expected if species are distributed independently on environmental gradients, rather than if assemblages consist of highly co-evolved, interdependent species. The observed spatial patterns were highly persistent through time. There are regions which are relatively homogeneous with regard to species composition and which can therefore be useful in dealing with bycatch problems. However, this study does not indicate the existence of discrete assemblages which might be appropriate as ecologically based fishery management units.

Cette étude est basée sur dix-huit levés (douze en été, trois au printemps et trois en automne) effectués au moyen de chaluts de fond dans la plate-forme Scotian et la baie de Fundy. La séquence de l'analyse des données était la suivante : aggrégation temporelle et spatiale des ensembles de chalut; estimation des indices de distance inter-espèces et inter-sites; groupement et ordonnancement des sites et des espèces; et discrimination des groupes de sites à l'aide des variables environnementales. Neuf groupe-espèces et 10 groupes-sites ont été définis et les données se rapportant à chacun d'eux ont été présentées dans un tableau à double entrée. La profondeur et la température étaient les variables environnementales les plus fortement associées aux différences dans la structure d'assemblage entre les groupes-sites. Les changements dans la structure d'assemblage d'une région à l'autre étaient distincts mais apparemment graduels, aucune limite nette d'assemblage n'apparaissant avec évidence. On doit s'attendre à cette configuration lorsque l'espèce est distribuée indépendamment des gradients environnementaux plutôt que lorsque les assemblages consistent en espèces interdépendantes en évolution fortement reliée. Les configurations spatiales observées étaient très stables dans le temps. Certaines régions sont relativement homogènes en ce qui a trait à la composition des espèces et peuvent donc être utiles pour résoudre les problèmes de prises fortuites. Cette étude ne révèle toutefois l'existence d'aucun assemblage discret qui pourrait servir d'unité de gestion des pêches basée sur l'écologie.

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Although most fisheries are managed on a single species basis, there is general recognition that interactions among species are an important factor which should be considered (Hobson and Lenarz 1977; Mercer 1982). There is a variety of multi-species approaches to management, in different stages of development as regards their practical application. Some examples are: the optimization of combined yield in mixed fisheries, ignoring biological interactions (Murawski 1983); surplus production modelling of an assemblage of coexisting species (Halliday and Doubleday 1976; Pauly 1979); and detailed models incorporating the dynamics of the important species and their environmental and biotic interactions (Anderson and Ursin 1977).

Whichever approach is adopted, it is necessary to delineate the community or assemblage for which the strategy should be developed. Ideally, the assemblage should be defined in such a way as to minimize the external influences and should be temporally persistent. Although it is frequently necessary to adopt an operational approach for management purposes, it is also important to consider the ecological basis for assemblage definition (Tyler et al. 1982).

The observation that the majority of studies of community structure and organization of terrestrial vertebrates over the past 20 y have been based on short surveys (Wiens 1981) applies also to fishes. In studies of fish communities much effort has been directed towards broad geographic comparisons (e.g. Barbour and Brown 1974; Gorman and Karr 1978; Horwitz 1978; Gladfelter et al. 1980; Ogden and Ebersole 1981; Rahel 1984; Mahon 1984) and to studies of resource partitioning (e.g. Werner et al. 1977; Sale 1977; Mendelson 1975; Baker and Ross 1981). Only recently have some studies addressed the question of resilience and persistence of assemblages of fishes from streams (Grossman et al. 1982; Mathews 1982; Herbold 1984; Moyle and Vondracek 1985), intertidal pools (Thompon and Lehner 1976; Grossman 1982), and coral reefs (Sale 1980; Ogden and Ebersole 1987). From this work has emerged a lively debate on the relative importance of stochastic and deterministic processes in structuring fish assemblages. Many methodological and conceptual problems remain unresolved, but the choice of spatial and temporal scales in defining assemblages for study is of clear importance (Anderson et al. 1981; Herbold 1984; Rahel et al. 1984). Connell and Sousa (1983) provide strict criteria for defining assemblages in studies of persistence and stability; however, few of these criteria have been met by any study as the information required is seldom available.

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In this paper, our three objectives are: to elucidate the spatial patterns of distribution of demersal fishes over a large area of continental shelf, the Scotian Shelf (Fig. 1); to evaluate the temporal persistence of this structure on interannual and seasonal time scales; and to examine the relationships between the patterns and the physical environment. The findings are directly relevant both to the management of the fisheries in the region and to a topical question in community ecology; that of temporal and spatial persistence of communities. The results of this study also provide a broad ecological context for the work on the demersal stage of commercially important fish species carried out during the Southwest Nova Scotia Fisheries Ecology Program.

This study is based on 12 yr of summer surveys and 3 yr each of spring and fall surveys with bottom trawls over the Scotian Shelf and in the Bay of Fundy. The main purpose of these trawl surveys has been to provide fishery independent indices of abundance for commercially important demersal species. Our approach to the analysis of these data is as follows: temporal and spatial aggregation of trawl sets; estimation of interspecies and intersite distance indices; clustering and ordination of sites and species, and discrimination of site groups using environmental variables. We first describe the patterns in the summer surveys, then compare them with those found in the spring and fall surveys.

Scotian Shelf and Bay of Fundy

The Scotian Shelf, it's slope, and the Bay of Fundy are the area under consideration (Fig. 1). The shelf is about 690 km long and from 110 to 120 km wide (Heezen et al. 1959). To the northeast it is separated from the Grand Banks of Newfoundland by the Laurentian Channel. To the southwest, the Northeast Channel separates the Scotian Shelf from Georges Bank and the Gulf of Maine. The topography of the Scotian Shelf is complex, as is typical of glaciated shelves (Uchupi

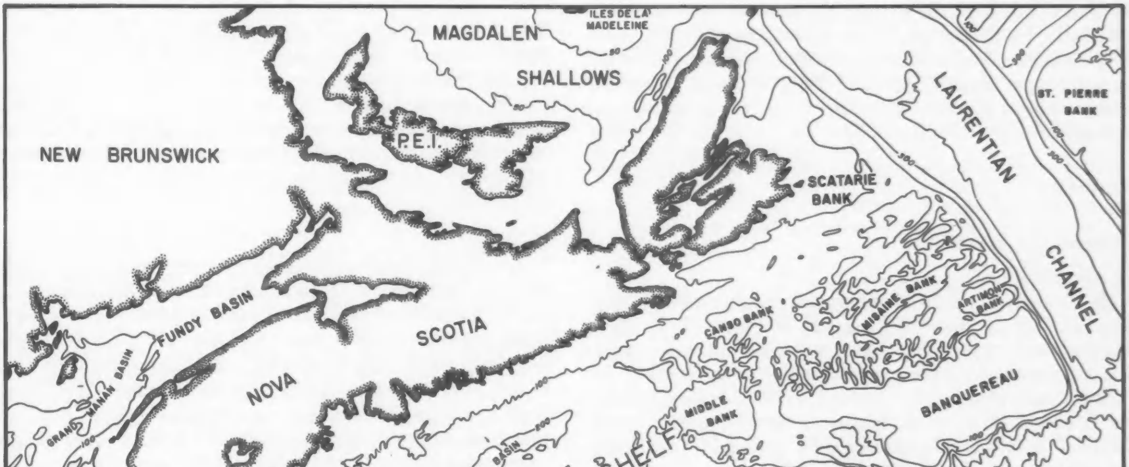
ILES DE LA MADELEINE
MAGDALEN SHALLOWS
P.E.I.
NEW BRUNSWICK
LAURENTIAN CHANNEL
ST. PIERRE BANK
SCATARIE BANK
FUNDY BASIN
NOVA SCOTIA
CANSO BANK
MISAINE BANK
ARTIMON BANK
GRAND MANAN BASIN
MIDDLE BANK
BANQUEREAU
SCOTIAN SHELF
SABLE I.
SABLE ISLAND BANK
THE GULLY
JORDAN BASIN
LAHAVE BASIN
SAMBRO BANK
EMERALD BASIN
ROSEWAY BANK
ROSEWAY BASIN
WESTERN BANK
EMERALD BANK
LAHAVE BANK
SCOTIAN SLOPE
BACCARO BANK
BROWNS BANK
SCOTIAN RISE
GEORGES BASIN
NORTHEAST CHANNEL
GEORGES BANK
50
100
200
500

FIG. 1. Scotian Shelf and Bay of Fundy.

1968). Along the coast is a rocky zone about 30 km wide. Seaward of this zone is a relatively flat area of intermediate depth (100–150 m) in which are several deep basins. Of these, the largest are Roseway (185 m), LaHave (269 m), and Emerald (291 m) Basins. To the northeast the basins are particularly dendritic. Along the outer edge of the shelf, several flat-topped banks of various sizes are separated by low saddles.

In the southwest, the study area includes parts of the Georges and Jordan Basins, and the entire Bay of Fundy which is about 250 km long and from 50–100 km wide. Depths in the latter range from about 50 m near the head to about 150 m near the mouth where there are a few deep holes.

The circulation and water characteristics of the Scotian Shelf are complex, in keeping with the topography, and the fact that the waters originate from three main sources: the outflow of the St. Lawrence River into the Gulf of St. Lawrence, the Labrador Current, and North Atlantic water (Houghton et al. 1978; Trites and Loucks 1985). The last of these includes water from the Gulf Stream and the central North Atlantic. In summary Labrador Current water enters the Gulf of St. Lawrence where it mixes with the river outflow, then flows out through the Cabot Strait and along the Scotian Shelf parallel to the coast as the Nova Scotian Current (Sutcliffe et al. 1976). The fate of this water as it moves onto the southwestern half of the shelf is poorly known. Some is apparently diverted offshore (Smith 1983) and some continues along the coast, turning northwest around the southern tip of Nova Scotia. The water of the Nova Scotian Current is relatively cold with moderate salinity. As it moves along the shelf it mixes with warm, saline water from the shelf slope, particularly in the region of the Scotian Gulf at mid-shelf (Houghton et al. 1978). In the Bay of Fundy, water from the Gulf of Maine enters on the south side and exits along the north shore towards Cape Cod (Bigelow 1927). One of the most prominent features of the Bay of Fundy is extensive tidal mixing.

Methods

Preparation of Survey data

Survey procedures

The data are catches taken on research vessel groundfish trawl surveys of the Scotian Shelf and Bay of Fundy (Table 1). A stratified random sampling design was used in these surveys, with stratification by depth and geographic location (see Fig. 1). Further details are given by Doubleday (1981) and by Halliday and Koeller (1981). For the summer surveys, aboard RV *A.T. Cameron*, a Yankee 36 trawl was used, whereas for the spring and fall surveys, aboard RV *Lady Hammond*, a Western IIa trawl was used.

The target duration (on bottom) and average speed for each tow were 30 min and 3.5 knots. This give a 'standard tow' of 1.75 nautical miles. When duration or speed varied from the target values, the catch of each species was adjusted to catch per 'standard tow' by the factor 1.75/actual distance towed.

The spring and fall surveys were conducted during the fourth period only (1978–81). However, they will be compared with the overall patterns described for summer. Although spring and fall surveys were conducted with a different vessel and trawl to the summer surveys, an analysis of species composition in comparative fishing experiments has shown that it is valid to compare the results from these two vessels (Mahon and Smith 1989).

TABLE 1. Details of the surveys included in this analysis. There are two cruises per survey. A = A.T. Cameron, H = Lady Hammond.

Cruise ID	Dates	Number of stations analysed
A175/A176	July 6–July 31 1970	67/73
A188/A189	June 29–July 22 1971	52/61
A200/A201	June 23–July 19 1972	66/84
A212/A213	July 9–Aug. 3 1973	65/78
A225/A226	July 8–Aug. 3 1974	80/80
A236/A237	July 15–Aug. 6 1975	72/71
A250/A251	July 12–Aug. 5 1976	64/77
A265/A266	July 9–July 30 1977	91/54
A279/A280	July 9–Aug. 4 1978	79/63
A292/A293	July 6–July 27 1979	80/72
A306/A307	July 7–July 27 1980	63/85
A321/A322	July 4–July 25 1981	70/74
H013/H014	Mar. 5–Mar. 29 1979	43/77
H026/H027	Oct. 15–Nov. 8 1979	68/70
H033/H034	Mar. 5–Mar. 27 1980	49/58
H042/H043	Sep. 30–Oct. 22 1980	69/72
H048/H049	Feb. 23–Mar. 19 1981	73/48
H043/H066	Sep. 30–Oct. 22 1981	64/65

Selection of sites and species

Only trawl tows within the area comprising strata 40–95, Scotian Shelf and Bay of Fundy, were used in this analysis (see Fig. 11). Tows of less than 20 min in duration were excluded.

There were 91 demersal fish species (or groups of species; e.g. *Sebastes* spp.) in the tows which were retained for analysis (Mahon et al. 1984). Of these, only 31 were sufficiently abundant to be included in the analysis (Table 2). They each contributed more than 0.1% to either total numbers or total weight, or more than 0.05% to both total numbers and total weight.

The average depth of each tow was determined by echosounder. Bottom temperature was determined by mechanical or expendable bathythermograph and by reversing thermometer. Salinity was determined by titration or with a conductivity salinometer.

Sediment

A sediment type was assigned to each station using charts (Drapeau and King 1971; Fader et al. 1977, 1982; King 1970; MacLean and King 1971; MacLean et al. 1977). The approximate amounts of gravel, sand, silt, and clay in each sediment type were taken from King (1967). Because of the variability in and uncertainty about the percent contribution of each size-fraction to each sediment type we felt that an analysis based on ranks was most appropriate. Full details of the analysis of sediment data are given by Mahon et al. (1984) and are summarized following.

The sediment size-fractions were ranked according to particle size (gravel = 4, sand = 3, silt = 2, clay = 1). Then, the sediment types were ranked within each size fraction. For example, Sable Island sand and gravel contained the most gravel (75%) and received the highest rank value for this fraction. A sediment type which contained none of a particular size-fraction was given a rank of zero for that fraction.

These data were used to calculate a weighted mean and standard deviation for sediment size for each sediment type. That is, a mean size-fraction rank weighted by the ranks within size fractions (Table 3). The weighted mean was taken as an index of particle size in the sediment type and the standard deviation as an index inversely proportional to sorting.

TABLE 2. Number of individuals, total weight (kg) and frequency of capture (number of tows in which it was present) for the species included in the analysis. *Weights not always taken.

Species	Numbers	Weight	Frequency
Redfish, *Sebastes* spp.	169 061	5 963	974
Haddock, *Melanogrammus aeglefinus*	130 403	9 103	1 401
Silver hake, *Merluccius bilinearis*	82 184	1 413	1 085
American plaice, *Hippoglossoides platessoides*	66 028	2 145	1 766
Yellowtail flounder, *Limanda ferruginia*	60 126	1 512	886
Atlantic cod, *Gadus morhua*	59 259	6 870	1 792
Northern sand lance, *Ammodytes dubius*	24 640	82	63
Thorny skate, *Raja radiata*	18 438	1 796	1 790
White hake, *Urophysis tenuis*	16 498	1 803	1 059
Longhorn sculpin, *Myoxocephalus octodecemspinosus*	13 882	286	807
Spiny dogfish, *Squalus acanthias*	12 742	2 693	381
Witch flounder, *Glyptocephalus cynoglossus*	12 416	620	1 105
Atlantic argentine, *Argentina silus*	9 592	222	375
Pollock, *Pollachius virens*	8 264	2 436	559
Longfin hake, *Urophysis chesteri*	7 989	75	255
Winter skate, *Raja ocellata*	3 867	792	403
Winter flounder, *Pseudopleuronectus americanus*	3 188	198	257
Red hake, *Urophysis chuss*	2 642	71	281
Smooth skate, *Raja senta*	2 611	125	782
Vahl's eelpout, *Lycodes vahli*	2 394	33	97
Sea raven, *Hemitripterus americanus*	1 808	219	513
Mailed sculpin, *Triglops murrayi*	1 711	*	228
Atlantic wolffish, *Anarhichas lupus*	1 645	426	542
Angler, *Lophius americanus*	1 528	554	666
Cusk, *Brosme brosme*	1 197	358	401
Atlantic halibut, *Hippoglossus hippoglossus*	1 159	333	504
Ocean pout, *Macrozoarces americanus*	1 087	73	370
Common grenadier, *Nezumia bairdi*	991	*	775
Eelpouts, *Lycodes* spp.	966	*	86
Little skate, *Raja erinacea*	496	38	91
Barndoor skate, *Raja laevis*	122	50	26

TABLE 3. Percent contribution of each sediment fraction to each sediment type (above slash) and the rank of each sediment type within sediment fractions (below slash).

	Sediment fraction					
Sediment type	Gravel (4)	Sand (3)	Silt (2)	Clay (1)	Mean size	SD
Sable Island sand and gravel (>50% gravel)	75/7	25/2	0/0	0/0	3.78	0.42
(undetermined)	25/5	75/7	0/0	0/0	3.42	0.42
(<50% gravel)	50/6	50/4	0/0	0/0	3.60	0.49
Sambro sand	15/4	68/6	13/4	4/4	2.56	1.07
Scotian Shelf drift	3/3	64/5	17/5	16/5	2.33	1.05
Laurentian silt	0/0	30/3	47/7	23/6	1.81	0.73
Lahave clay	0/0	3/1	39/6	58/7	1.57	0.62

TABLE 4. Correlations of the sediment variables with the first three principal components (PC).

	PC1 SEDSIZE	PC 2 SEDSAND	PC 3 SEDSORT
1. Clay	−0.89	−0.22	−0.40
2. Silt	−0.89	−0.17	−0.41
3. Sand	+0.22	+0.96	−0.15
4. Gravel	+0.99	+0.13	+0.08
5. Mean Size	+0.94	+0.15	+0.29
6. SD	−0.34	+0.22	+0.91
Eigenvalue	3.60	1.10	1.28
Percent of total variance	60.0	18.3	21.3

Because the six variables in Table 3 were highly intercorrelated, we transformed them to three new independent variables with principal components analysis (Cooley and Lohnes 1971). The scores on the first three axes were used as values for these new variables. These axes were interpreted by examining the correlations between the sediment variables and the principal component scores on each axis (Table 4). The first principal component is highly correlated with gravel and mean size and highly negatively correlated with clay and silt. Thus, since samples with generally coarser sediment will have higher scores and those with finer sediment will have lower scores on principal component axis 1, we call this variable SEDSIZE. The scores on axis 2 are primarily correlated with the amount of sand, and we call this variable SEDSAND. The third principal component axis is chiefly negatively correlated with the standard deviation of the sediment size distribution. Sediments with high scores on this axis will be poorly sorted, and we call this variable SEDSORT.

In the subsequent analyses correlating sediment (and other variables) with the fish distributions, each station received the scores, or values, for each new sediment variable which correspond to the type of sediment shown at the station's position on the charts of sediment types.

Data Analysis

Aggregation of trawl sets

In order to include the entire area and time span in a single analysis which could reveal both the spatial pattern and its behaviour through time, it was necessary to reduce the amount of data by aggregating trawl sets. Sets were aggregated within sampling strata because the preliminary analysis had indicated that the scale of the spatial pattern was larger than these units. Data were also aggregated into four periods of three years each:

Period 1 1970–72,
Period 2 1973–75,
Period 3 1976–78,
Period 4 1979–81.

Before aggregation, each species' abundance was standardized within seasons and years to the species' mean value in all sets in which it occurred. This was done to take account of substantial changes in total abundance of some species through the time-series (see below).

The final data matrix consisted of 48 strata in each of four periods for the summer, and also for the spring and fall in period 4.

The environmental data were similarly aggregated but were not standardized as there was no indication of trends in temperature or salinity.

Hierarchical classification

Hierarchical classification displays the relationships between entities (the units being classified) with a two-dimensional hierarchical dendrogram. Agglomerative classification successively fuses the most similar entities, or groups of entities, to form larger groups or clusters (Clifford and Stephenson 1975). The computations utilise a matrix of dissimilarity (or similarity) indices to quantify the relationships among entities. In the present study we use the flexible clustering method (Lance and Williams 1967; Boesch 1977) with the flexible coefficient Beta set to the usual value of -0.25, to classify both the strata and the species.

Two-way coincidence tables

The dendrograms from the site and species classification analyses were used to construct two-way coincidence tables, which are simply the biological data matrix with the rows (species) and colums (sites) arranged in the same order as on the corresponding dendrograms. The data values were standardized and converted to symbols for compactness and ease of interpretation. The symbols in this study were based on species mean (of values >0) standardized data.

Two-way tables are informative and valuable because similar sites and species are grouped, and appear in contiguous positions in the table. As a result, biological patterns can easily be seen and interpreted. In addition, reference to the table is very useful when choosing groups from the dendrograms.

In order to discuss the way in which species and strata have clustered, and the changes in the membership of clusters through time and season, it is necessary to refer to the dendrograms as well as to the two-way tables. The dendrograms show the relationships among entities (species and strata) and groups of entities, whereas the two-way tables provide detailed information about the relative abundances on which the groupings are based.

Constancy and fidelity are attributes which can be used to summarise the relationships between species and site groups (Stephenson et al. 1972). The two-way table was used to estimate these attributes as described by (Colvocoresses and Musick 1984). Constancy is the ratio of observed to possible occurrences of a species group in a site group. Fidelity is the ratio of constancy of a species group in a site group to its average constancy in all other site groups. Fidelity substantially >1 indicates that the species group is highly characteristic of the site group.

Multiple discriminant analysis

Correlations between classification groups and environmental parameters were studied with multiple discriminant analysis (Cooley and Lohnes 1971; Hope 1969), as canonical analysis of discriminance. As in Smith (1976); Green and Vascotto (1978); and Bernstein et al. (1978), classification techniques were used to generate the groups used in the analysis. Weighted discriminant analysis (Smith 1976, 1989; Mahon et al. 1984; Smith et al. 1988) was used to increase the sensitivity of the analysis to information from the classification analysis about the strength of group membership, group cohesiveness, and intergroup relationships.

The stations or strata (depending on the particular analysis) are represented as points in a multidimensional space defined by the environmental variables. These points are projected onto axes that minimize the within-group variation while maximizing the between-group variation. These axes are independent and are correlated with the variables potentially important in the group separation. The environmental variables correlated with the axes are indicated with coefficients of separate determination (Hope 1969).

Results

Trends in Abundance

The trends from summer surveys for the 31 species included in this analysis are shown in Fig. 2. Catch per unit effort in the commercial fishery, and the results of cohort analyses corroborate the trawl survey trends for the dominant species; cod (Campana and Simon 1986; Sinclair and Annand 1986), haddock (Mahon et al. 1985; O'Boyle and Gregory 1985), pollock (McGlade et al. 1986), silver hake (Waldron et al. 1985). For cod and haddock the recovery of biomass in the late 1970s is clear. Other species, e.g. halibut and pollock, show similar patterns. Only redfish shows a steady decline in abundance through the period of the surveys. A few species, thorny skate, smooth skate, cusk and witch show distinct peaks in the middle of the 12 yr period. For the remaining species, the interannual variability is such that trends are not discernible.

Clustering of Species and Strata through Time

The combined analysis of all summer surveys resulted in nine species groups (Fig. 3). The definition of these is subjective, because there is no test for the level at which a group should be considered functionally insignificant (Gabriel and Murawski 1985). To evaluate the stability of species groups through the series of summer surveys and between seasons, we compare the overall summer species groups (Fig. 3) with the separate summer periods (Fig. 4) and with the spring and fall in period 4 (Fig. 5).

The survey strata tended to be very similar to themselves through the four summer time periods over the 12 yr of surveys (Fig. 6). Also, adjacent strata tend to group together, resulting in a spatial mosaic at a larger scale than that of the individual stratum. Spring and fall stratum clusters similarly show a tendency for adjacent strata to cluster together (Fig. 7).

The biological basis for these clusters is most clearly seen in the two-way tables showing the abundance of each species, rel-

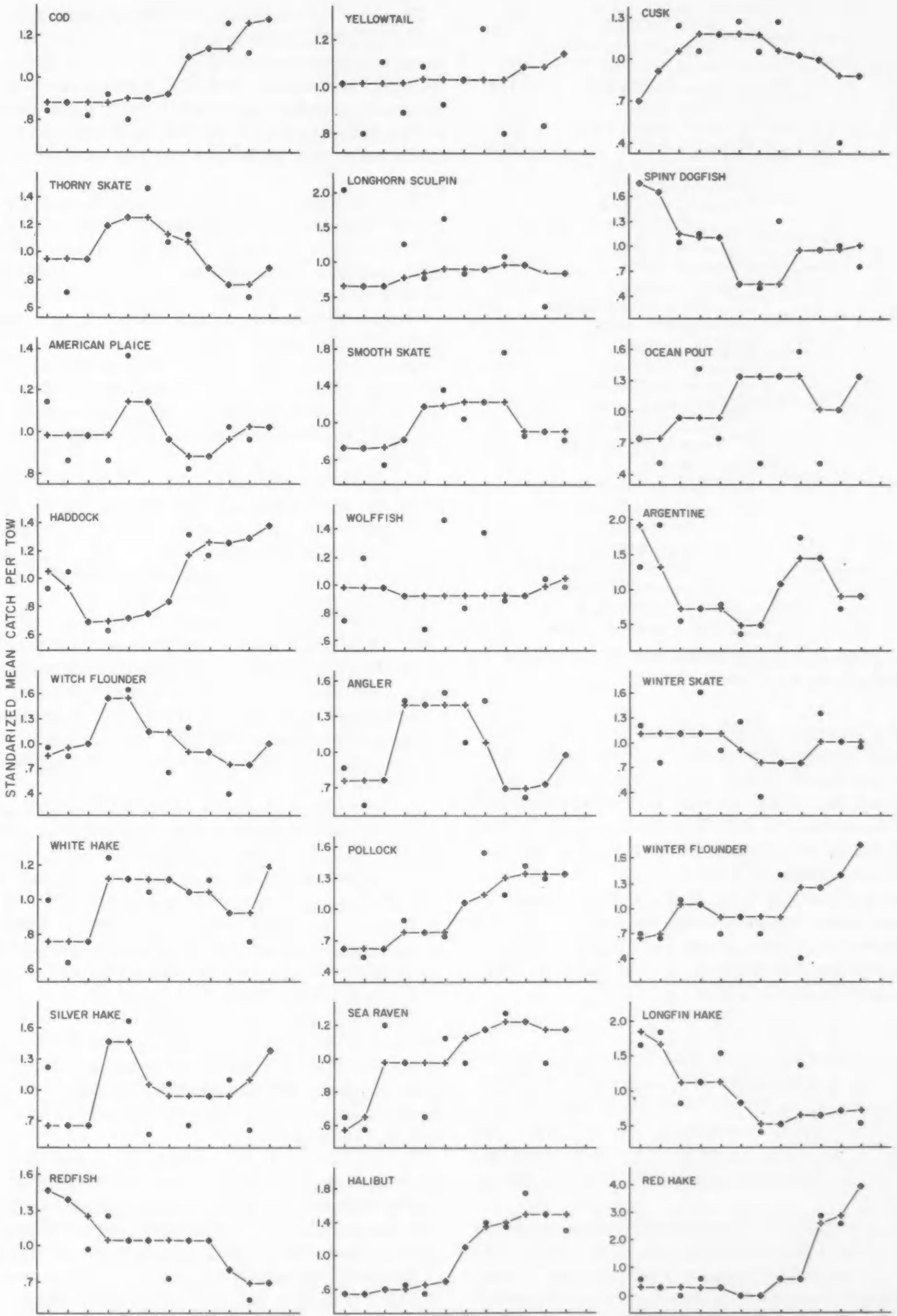

FIG. 2. Trends in trawl survey catch per unit effort for the major demersal species on the Scotian Shelf from 1970–81. The line and crosses show the median smoothed trend of the annual data points (solid circles), diamonds show where data points and median smoothed values coincide.

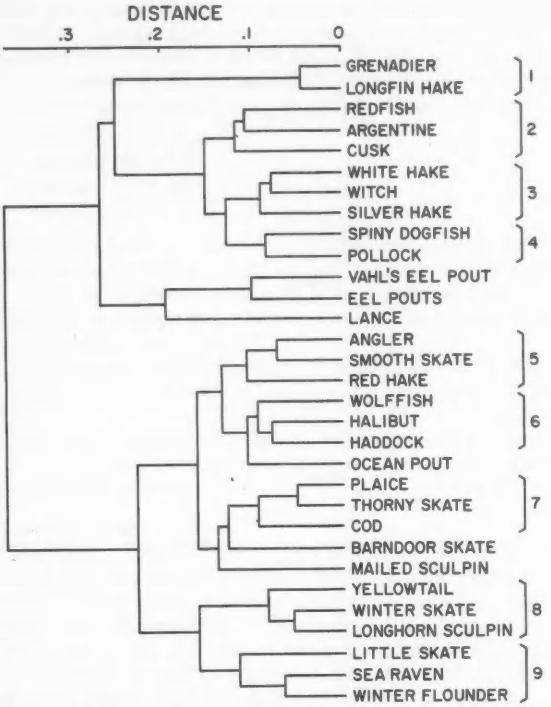

FIG. 3. Species groups (1–9) as determined from cluster analysis of all summer surveys combined.

ative to its mean for values >0 (Figs. 8 and 9). In these tables, the major stratum clusters (Figs. 6 and 7) are separated by vertical lines, and the species groups (Fig. 3) by horizontal lines. In spring and fall, the overall summer species groupings are used in the two-way tables for ease of comparison (Fig. 9). The constancy and fidelity of the species groups in the summer stratum groups are summarized in Table 5.

For this two-way analysis, there are three major issues: (1) how well strata cluster together through the four periods; (2) the spatial integrity of stratum-groups; and (3) the integrity of species groups. In the following sections, numbers in parentheses refer to stratum numbers from Fig. 11.

Stratum-groups (Figs. 6 and 8)

Group 1 (Northeast mixed) — This is the group to the extreme left of Fig. 8. It is comprised of strata 41–45 in all four periods and includes strata 57 and 59 in two periods and one period, respectively. These constitute an area of mixed and medium depths in the Northeast corner of the shelf. They are characterized by plaice/thorny skate/cod, by eelpouts, and by mailed sculpin.

Group 2 (Eastern Banks) — This includes Banquereau Bank (47, 48), Sable Island Bank (55, 56), and Middle Bank (58). Western Bank (64) and the deeper water between Sable Island and Middle Banks (57) are each included for one period. In this stratum-group plaice/thorny skate/cod remains strong and is joined by yellowtail flounder/winter skate/longhorn sculpin. It would be reasonable to further subdivide this group into Banquereau and other areas, with the Gully as the physical boundary. The biological basis for the subdivision would be the presence of little skate/sea raven/winter flounder to the west of the Gully.

Group 3 (Bay of Fundy) — This includes strata 90–95 for all periods and the outer reaches (85) in two periods. This group is closest in species composition to the eastern banks. The major difference is that in this area little skate/sea raven/winter flounder appear to replace yellowtail flounder/winter skate/longhorn sculpin and spiny dogfish/pollock are most evident. This is also the area of greatest abundance, constancy and fidelity, for ocean pout.

Group 4(Western Banks) — This comprises the remaining banks; Western (64 in three periods), Emerald (63), LaHave (73), Roseway (74), Baccaro (75), and Browns (80). The major difference from the eastern banks is that wolffish/halibut/haddock is the most prominant, whereas plaice/thorny skate/cod, although very constant here as elsewhere, are less abundant than to the east of this group of strata.

Group 5 (Southeast corner) — Strata 49 and 50, the shelf break and slope at the eastern corner comprise this small group. Plaice/thorny skate/cod are the main species group here. Here smooth skate is locally most abundant, independent of its group members.

Group 6 (Outer central) — This is almost entirely comprised of middle depth strata (51–100 fathoms) on the outer central and western shelf. The exception is stratum 53 for one period. None of the species groups really stand out in this stratum-group. This is one of three stratum-groups with high constancy for wolffish/halibut/haddock.

Group 7 (Inner central) — these are middle and mixed depth (59) strata from the inner central and western shelf. Redfish alone of redfish/argentine/cusk is abundant here. Similarly, pollock of pollock/spiny dogfish is relatively abundant. Two other groups, white hake/witch/silver hake and angler/smooth skate/witch contribute most to the catch. However, as for the previous stratum-group, no species group shows strong fidelity (Table 5).

Group 8 (Shelf basins) — Emerald (61) and LaHave (71) Basins are included in all periods, and shallower adjacent strata (70, 62, 60, 66) in some periods. Of these, stratum 76 (3 periods) contains the Roseway Basin. Stratum 84, the Jordan/Georges Basins, is included for one period. This group of strata is most closely related to the seventh, and is therefore similar in species composition. Redfish/argentine/cusk and white hake/witch/silver hake are constant, but only the former species group shows high fidelity (Table 5).

Group 9 (Northeast Channel and basins) — The Northeast Channel (87), Georges (93), and Jordan (84) Basins, and the adjacent stratum (85) off the southwest tip of Nova Scotia comprise this group. The main difference between this area and the previous two, lies in the relatively high fidelity of spiny dogfish/pollock (Table 5).

Groups 10 and 11 (Laurentian Slope and Outer slope) — These are comprised primarily of deep-slope strata. The Gully groups with the Laurentian Channel strata because argentine and cusk are scarce there. Longfin hake/grenadier characterises (high fidelity) these stratum-groups.

An overall perspective of the sequence of stratum-groups from left to right is that they lie along a gradient of increasing depth (Fig. 8). The role of depth in assemblage organization will become more evident with the discriminant analysis. Discussion of the larger scale affinities of stratum-groups, and of the faunal and environmental differences underlying these have been deferred to that section.

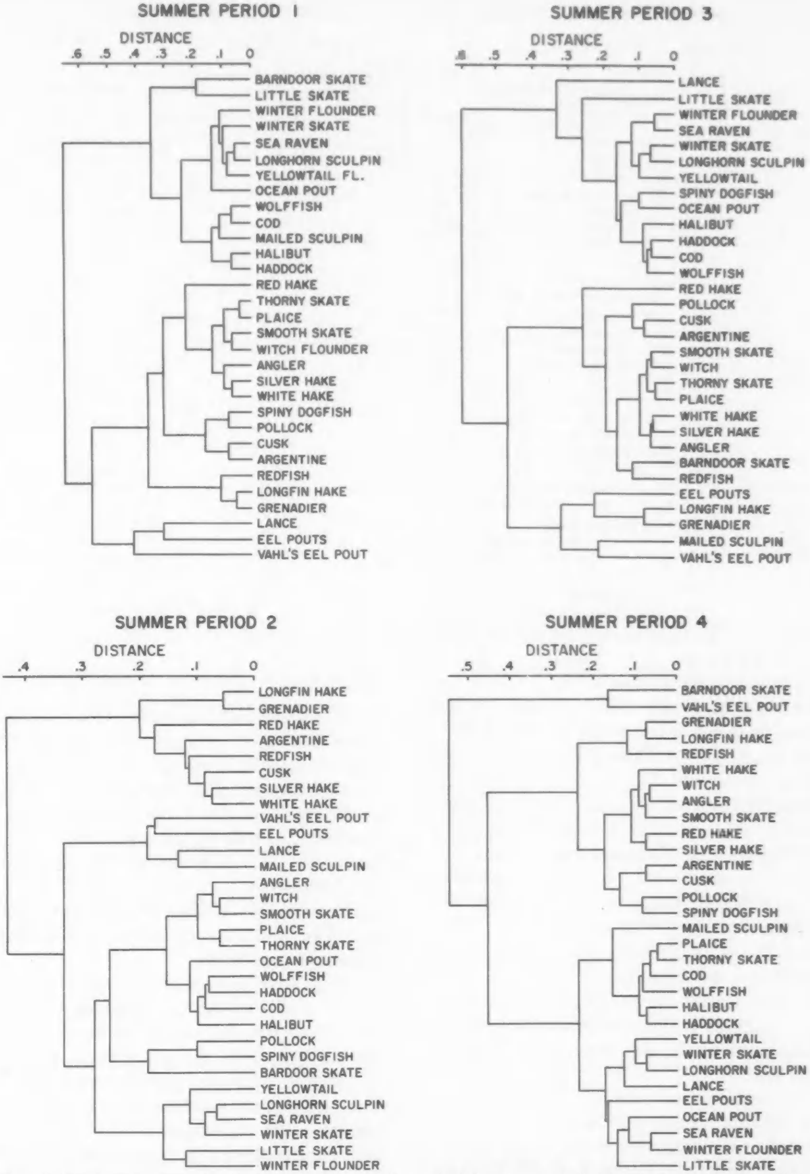

FIG. 4. Clustering of species during summer within each of the four periods (1970–72, 1973–75, 1976–78, 1979–80).

Species groups

The above description of stratum-groups outlines the spatial distribution of species and species groups, but does not specifically evaluate the stability of the species groups over the years. (Fig. 4) and between seasons (Fig. 5). In the following sections we do this with reference to the overall summer groupings (Fig. 3).

Longfin hake/grenadier — This deep water pair shows close association in all four summer periods, and in the spring and fall.

Redfish/argentine/cusk — Argentine and cusk cluster directly in periods 2, 3, 4, and indirectly in period 1. The common distribution of these two species is evident in Fig. 8, which also shows that redfish frequently occur where the other two group members do not, this is true also in spring and fall (Fig. 9). Redfish clusters with longfin hake/grenadier in two time periods (Fig. 4). Argentine and cusk also cluster directly in spring, but not fall, when the latter is more widely distributed.

White hake/witch/silver hake — The first two species in this group are closely associated in all three seasons, and are joined by silver hake in summer.

Spiny dogfish/pollock — This association is found in summer, based primarily on their co-occurrence in the Bay of Fundy and Northeast channel. Although in fall pollock are still found

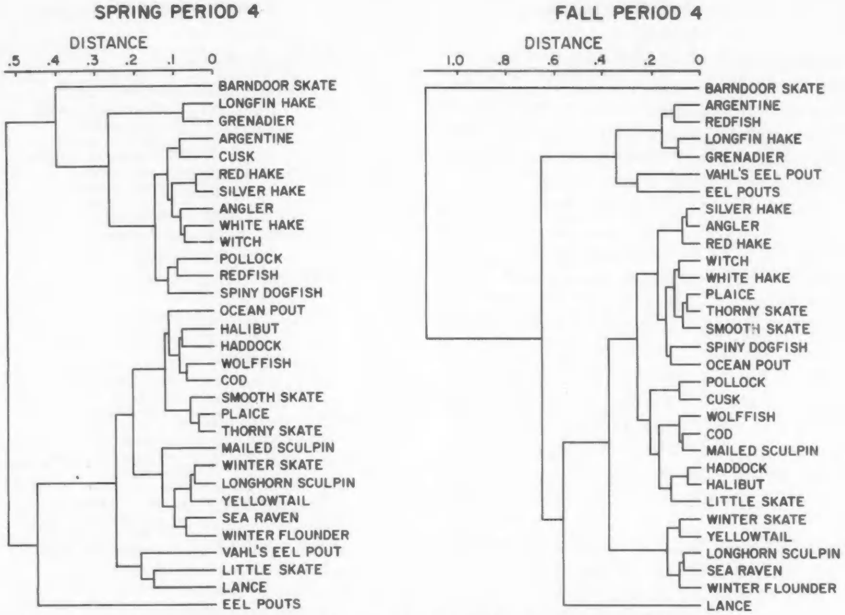
SPRING PERIOD 4
DISTANCE
.5 .4 .3 .2 .1 0
BARNDOOR SKATE
LONGFIN HAKE
GRENADIER
ARGENTINE
CUSK
RED HAKE
SILVER HAKE
ANGLER
WHITE HAKE
WITCH
POLLOCK
REDFISH
SPINY DOGFISH
OCEAN POUT
HALIBUT
HADDOCK
WOLFFISH
COD
SMOOTH SKATE
PLAICE
THORNY SKATE
MAILED SCULPIN
WINTER SKATE
LONGHORN SCULPIN
YELLOWTAIL
SEA RAVEN
WINTER FLOUNDER
VAHL'S EEL POUT
LITTLE SKATE
LANCE
EEL POUTS
FALL PERIOD 4
DISTANCE
1.0 .8 .6 .4 .2 0
BARNDOOR SKATE
ARGENTINE
REDFISH
LONGFIN HAKE
GRENADIER
VAHL'S EEL POUT
EEL POUTS
SILVER HAKE
ANGLER
RED HAKE
WITCH
WHITE HAKE
PLAICE
THORNY SKATE
SMOOTH SKATE
SPINY DOGFISH
OCEAN POUT
POLLOCK
CUSK
WOLFFISH
COD
MAILED SCULPIN
HADDOCK
HALIBUT
LITTLE SKATE
WINTER SKATE
YELLOWTAIL
LONGHORN SCULPIN
SEA RAVEN
WINTER FLOUNDER
LANCE

FIG. 5. Clustering of species during spring and fall in period 4 (compare with Fig. 3).

in the Bay of Fundy, they tend to be more abundant out on the Scotian Shelf, at intermediate depths. Spiny dogfish are relatively scarce in spring, as they migrate south for the winter.

Angler/smooth skate/red hake — These species do not hold together as a group in spring and fall. Even in summer, red hake does not consistently co-occur with the first two species.

Haddock/halibut/wolffish — This trio persists as a group in spring and fall, when haddock and halibut continue to occur as a pair. In spring these three species are joined by cod, whereas in fall the association with wolffish is looser, including cod, mailed sculpin and little skate in a larger group.

Plaice/thorny skate/cod — The first two species of this group cluster directly in all four summer periods as well as in spring and fall. However, examination of the individual summer periods indicates that cod tends to cluster with members of haddock/halibut/wolffish, particularly the latter. This tendency persists in spring and fall.

Yellowtail/winter skate/longhorn sculpin — This shallow-water group is identifiable in all summer periods as well as in spring and fall, but shifts in membership of the clusters reflect the similar distribution of little skate/sea raven/winter flounder.

The two-way table (Fig. 8) also provides a means to evaluate the validity of the species groupings, on the basis of their stability in space as well as time. In most groups one or more of the species have areas of high abundance where the other group members are absent or scarce. Redfish/argentine/cusk is a notable example with redfish being abundant in Group 10 (Laurentian slope) and the other two species being rare. The white hake/witch/silver hake combination breaks down in stratum Groups 1 and 10. Similarly, wolffish/halibut/haddock breaks down in Group 1. Yellowtail/winter skate/longhorn sculpin breaks down in the Bay of Fundy where the first and last members are rare and abundant, respectively. On the other hand, although plaice/thorny skate/cod is ubiquitous, the relative abundance of the group members covaries. Grenadier/longfin hake is the most obvious common distribution.

Disciminant Analysis of Stratum-Groups in Summer

The objective of this analysis was to determine the extent to which the stratum-groups, which are biologically based, could be discriminated using the environmental variables. The first two discriminant axes accounted for 69.6 and 18.6% of the group separation which was achieved (Table 6). Depth and temperature, respectively showed the strongest association with these axes. SEDSIZE, SEDSORT, and salinity were also associated with Axis 1, whereas SEDSIZE was associated with Axis 2. The third axis which accounted for a further 5.1% of group separation reflected variation in SEDSIZE and SEDSORT, independent of depth.

The stratum-groups are displayed in the space defined by Axes 1 and 2 of the discriminant analysis (Fig. 10). In this figure the arrow diagram shows the orientation of the main variables in relation to the axes. These were obtained by plotting the variables in the discriminant space. The location of the group in the space indicates the physical conditions which prevail in that area. The orientation of the long axis for elongate groups indicates the physical variable which varies most for that group. For example, depth varies most for the Laurentian Slope, whereas temperature varies least. Opposite conditions prevail for the Southeast Corner stratum-group.

In Fig. 10, the shallow banks and Bay of Fundy lie to the left, with the Eastern Banks being cooler and less saline than the Western Banks. The Bay of Fundy is split into two non-overlapping groups, primarily on the depth axis, with the lower right one consisting primarily of the Strata 91 and 92 in the mouth of the Bay. However, this difference is not reflected very strongly in the dendrogram, with the main difference being the scarcity of winter and little skate in deeper water. The most diffuse group is the Northeast Mixed which is characterized by cooler less saline water than the rest of the shelf.

The Outer and Inner Central stratum-groups overlap broadly in the center of Fig. 10, with the outer group being warmer.

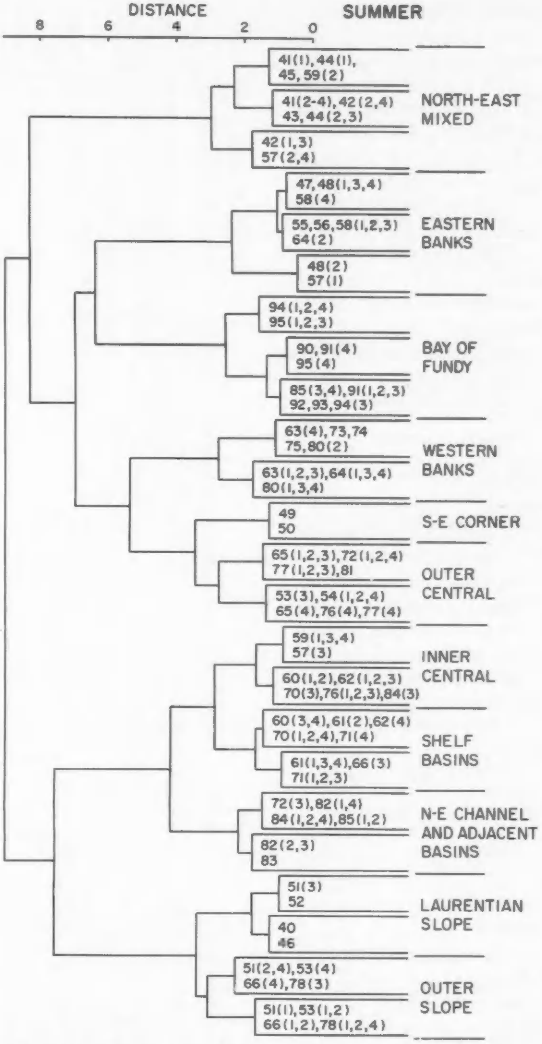
DISTANCE
SUMMER
8
6
4
2
0
41(1),44(1), 45,59(2)
41(2-4),42(2,4) 43,44(2,3)
42(1,3) 57(2,4)
NORTH-EAST MIXED
47,48(1,3,4) 58(4)
55,56,58(1,2,3) 64(2)
48(2) 57(1)
EASTERN BANKS
94(1,2,4) 95(1,2,3)
90,91(4) 95(4)
85(3,4),91(1,2,3) 92,93,94(3)
BAY OF FUNDY
63(4),73,74 75,80(2)
63(1,2,3),64(1,3,4) 80(1,3,4)
WESTERN BANKS
49 50
S-E CORNER
65(1,2,3),72(1,2,4) 77(1,2,3),81
53(3),54(1,2,4) 65(4),76(4),77(4)
OUTER CENTRAL
59(1,3,4) 57(3)
60(1,2),62(1,2,3) 70(3),76(1,2,3),84(3)
INNER CENTRAL
60(3,4),61(2),62(4) 70(1,2,4),71(4)
61(1,3,4),66(3) 71(1,2,3)
SHELF BASINS
72(3),82(1,4) 84(1,2,4),85(1,2)
82(2,3) 83
N-E CHANNEL AND ADJACENT BASINS
51(3) 52
40 46
LAURENTIAN SLOPE
51(2,4),53(4) 66(4),78(3)
51(1),53(1,2) 66(1,2),78(1,2,4)
OUTER SLOPE

FIG. 6. Clustering of strata in summer through the four periods, and definition of stratum-groups (Northeast mixed through Outer Slope).

The shelf basins and the outer slope of the shelf are well separated on these two axes, which indicate that the former is shallower, warmer, and less saline. These two groups are broadly overlapped by the Northeast Channel and adjacent basins. The slope of the Laurentian Channel, is also distinctly cooler and less saline than that of the outer Scotian Shelf.

Although Axis 3 does not contribute much to overall group separation, shallow stratum-groups, particularly Bay of Fundy and Western Banks are widely separated on that axis. This suggests that sediment particle size and degree of sorting may be determinants of assemblage structure at shallow depths on the shelf.

Summarizing the Spatial Pattern

Although the clusters of strata in periods were relatively stable in terms of their composition through time, there were sufficient instances of apparent misclassification, or noise, to cast doubt as to the degree of persistence of assemblages in space and time. In this section, we look more closely at some of the apparent anomalies in classification. Then we reallocate stratum/periods among groups to provide a general picture of the spatial pattern of assemblages.

The plot of stratum-groups in discriminant space shows whether apparent misclassifications in Fig. 6 fit into their groups environmentally as well as biologically (Fig. 10), while the two-way table (Fig. 8) shows the biological differences which led to the apparent misclassifications.

In the Eastern Banks and Outer Central groups (Fig. 10), the single observations to the extreme right of each group are outliers as regards the environment, belonging with the Northeast Mixed group and with the Outer Shelf Slope group, respectively. In the first case (Stratum 57, period 1) the occurrence

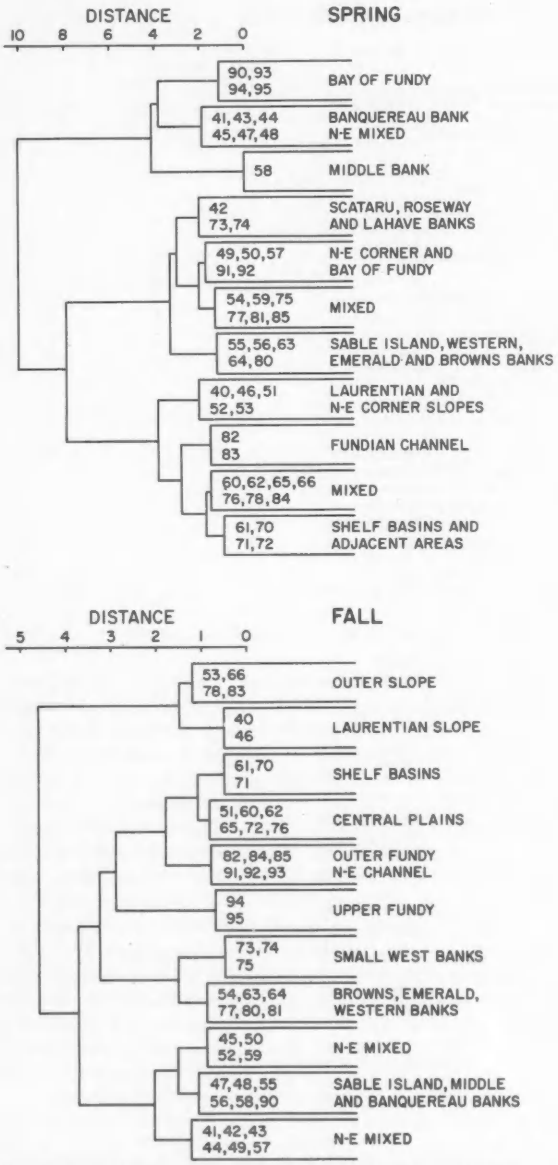
DISTANCE
SPRING
10 8 6 4 2 0
90,93 94,95
BAY OF FUNDY
41,43,44 45,47,48
BANQUEREAU BANK N-E MIXED
58
MIDDLE BANK
42 73,74
SCATARU, ROSEWAY AND LAHAVE BANKS
49,50,57 91,92
N-E CORNER AND BAY OF FUNDY
54,59,75 77,81,85
MIXED
55,56,63 64,80
SABLE ISLAND, WESTERN, EMERALD AND BROWNS BANKS
40,46,51 52,53
LAURENTIAN AND N-E CORNER SLOPES
82 83
FUNDIAN CHANNEL
60,62,65,66 76,78,84
MIXED
61,70 71,72
SHELF BASINS AND ADJACENT AREAS
DISTANCE
FALL
5 4 3 2 1 0
53,66 78,83
OUTER SLOPE
40 46
LAURENTIAN SLOPE
61,70 71
SHELF BASINS
51,60,62 65,72,76
CENTRAL PLAINS
82,84,85 91,92,93
OUTER FUNDY N-E CHANNEL
94 95
UPPER FUNDY
73,74 75
SMALL WEST BANKS
54,63,64 77,80,81
BROWNS, EMERALD, WESTERN BANKS
45,50 52,59
N-E MIXED
47,48,55 56,58,90
SABLE ISLAND, MIDDLE AND BANQUEREAU BANKS
41,42,43 44,49,57
N-E MIXED

FIG. 7. Clustering of strata in the spring and fall in time-period 4 (compare with Fig. 6).

of the yellowtail/winter skate/longhorn sculpin species group probably resulted in its classification with the Eastern Banks. In the second case (Stratum 53, period 3) the absence of longfin hake/grenadier was the probable reason for its exclusion from the Outer Shelf Slope group.

For the Laurentian Slope group there are two outliers above and to the left. The upper of these is an Outer Slope stratum (51-3) which was atypical of that group in that it lacked argentine and cusk and was consequently classified with the Laurentian Slope group (Fig. 6). The lower of the two points is actually a Laurentian Slope stratum (54-2) for which the environment sampled in that period differed from the rest of the group.

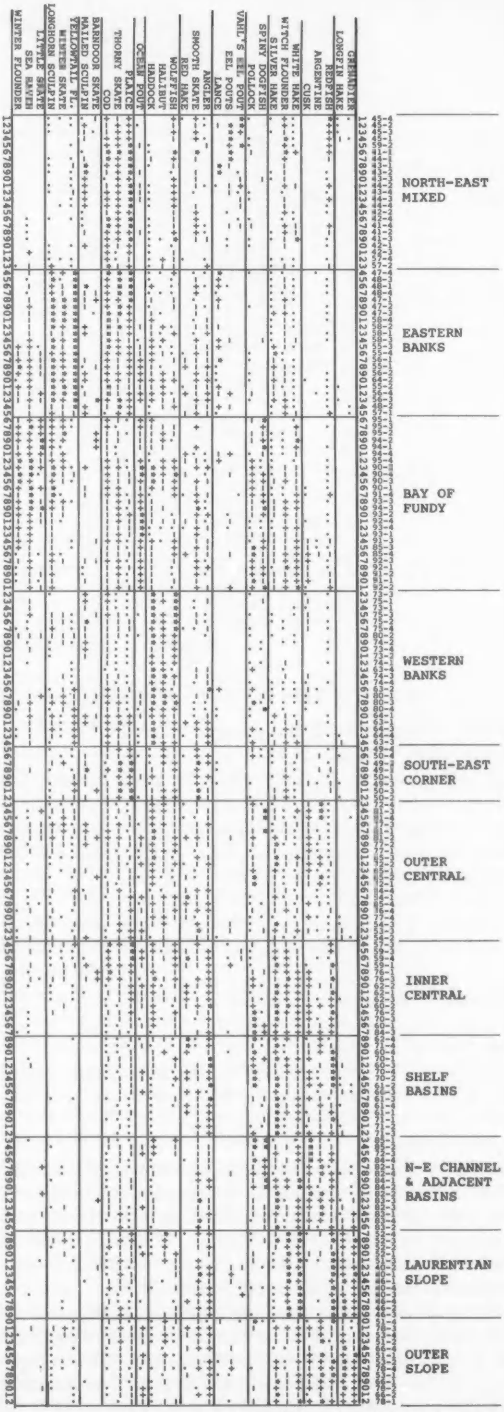
GRENADIER
LONGFIN HAKE
REDFISH
ARGENTINE
CUSK
WHITE HAKE
WITCH FLOUNDER
SILVER HAKE
SPINY DOGFISH
POLLOCK
VAHL'S EEL POUT
EEL POUTS
LANCE
ANGLER
SMOOTH SKATE
RED HAKE
WOLFFISH
HALIBUT
HADDOCK
OCEAN POUT
PLAICE
THORNY SKATE
COD
BARNDOOR SKATE
YELLOWTAIL FL.
MAILED SCULPIN
WINTER SKATE
LONGHORN SCULPIN
LITTLE SKATE
SEA RAVEN
WINTER FLOUNDER
NORTH-EAST MIXED
EASTERN BANKS
BAY OF FUNDY
WESTERN BANKS
SOUTH-EAST CORNER
OUTER CENTRAL
INNER CENTRAL
SHELF BASINS
N-E CHANNEL & ADJACENT BASINS
LAURENTIAN SLOPE
OUTER SLOPE

FIG. 8. Two-way table showing the relative abundance of species in the strata in summer for all four periods. Species and stratum-groups are arranged as shown in Figs. 4 and 6. The symbols show abundance relative to the species mean (blank = 0, · = 0–0.5, − = 0.5–1.0, + = 1.0–2.0, * = >2.0). The repeating series of numbers 0–9, above and below the main body of the table reference the columns.

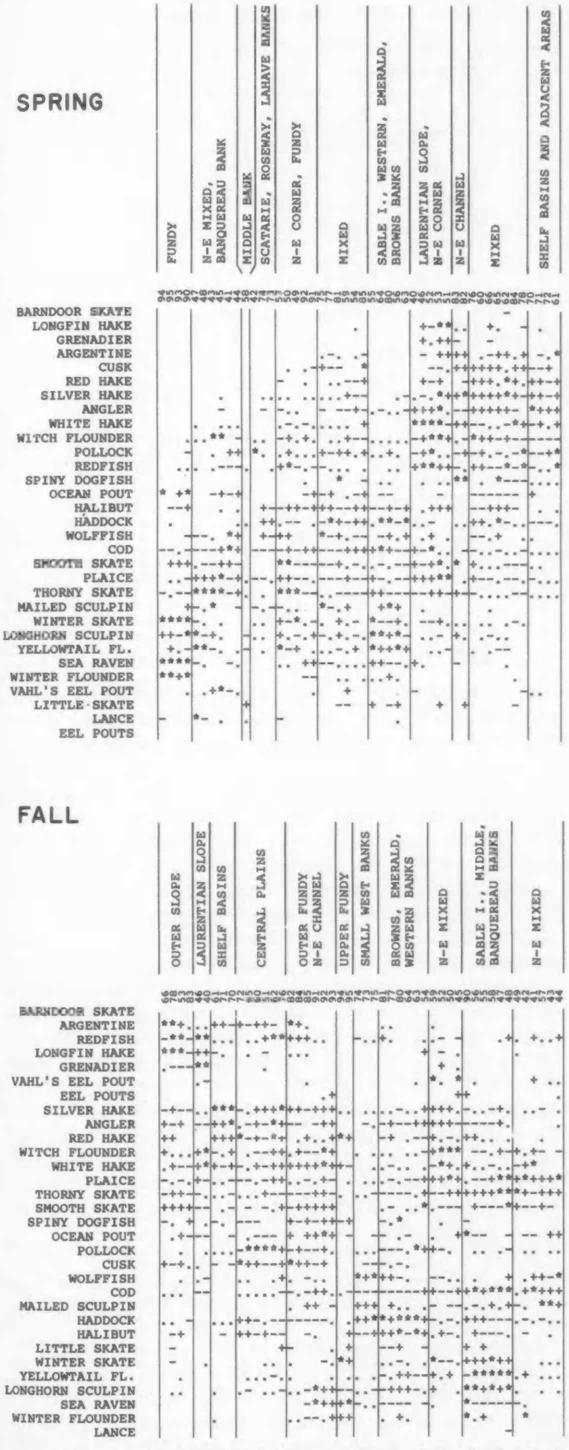
SPRING
FUNDY
N-E MIXED, BANQUEREAU BANK
MIDDLE BANK
SCATARIE, ROSEWAY, LAHAVE BANKS
N-E CORNER, FUNDY
MIXED
SABLE I., WESTERN, EMERALD, BROWNS BANKS
LAURENTIAN SLOPE, N-E CORNER
N-E CHANNEL
MIXED
SHELF BASINS AND ADJACENT AREAS
BARNDOOR SKATE
LONGFIN HAKE
GRENADIER
ARGENTINE
CUSK
RED HAKE
SILVER HAKE
ANGLER
WHITE HAKE
WITCH FLOUNDER
POLLOCK
REDFISH
SPINY DOGFISH
OCEAN POUT
HALIBUT
HADDOCK
WOLFFISH
COD
SMOOTH SKATE
PLAICE
THORNY SKATE
MAILED SCULPIN
WINTER SKATE
LONGHORN SCULPIN
YELLOWTAIL FL.
SEA RAVEN
WINTER FLOUNDER
VAHL'S EEL POUT
LITTLE SKATE
LANCE
EEL POUTS
FALL
OUTER SLOPE
LAURENTIAN SLOPE
SHELF BASINS
CENTRAL PLAINS
OUTER FUNDY N-E CHANNEL
UPPER FUNDY
SMALL WEST BANKS
BROWNS, EMERALD, WESTERN BANKS
N-E MIXED
SABLE I., MIDDLE, BANQUEREAU BANKS
N-E MIXED
BARNDOOR SKATE
ARGENTINE
REDFISH
LONGFIN HAKE
GRENADIER
VAHL'S EEL POUT
EEL POUTS
SILVER HAKE
ANGLER
RED HAKE
WITCH FLOUNDER
WHITE HAKE
PLAICE
THORNY SKATE
SMOOTH SKATE
SPINY DOGFISH
OCEAN POUT
POLLOCK
CUSK
WOLFFISH
COD
MAILED SCULPIN
HADDOCK
HALIBUT
LITTLE SKATE
WINTER SKATE
YELLOWTAIL FL.
LONGHORN SCULPIN
SEA RAVEN
WINTER FLOUNDER
LANCE

FIG. 9. Two-way tables of relative abundance of species in strata groups for spring and fall (symbols as in Fig. 8).

Other apparent misclassifications and environmentally anomalous points were tracked down and were all due to smaller differences in species composition than these described above. We consider that the differences leading to the apparent misclassifications are within the levels which could be expected from trawl sampling and that it would be appropriate to summarize the spatial pattern by reclassifying the anomalous observations (stratum periods) to provide a spatially coherent picture of assemblages over the 12 yr period (Fig. 11).

In this summary we retain the original names given to the stratum-groups. In most instances the decision to reallocate a stratum period was easily made, for example, the reallocation of 59-1 from the Northeast Mixed to the Inner Central group (Fig. 6). Some choices were much less clear. The two main examples are whether stratum 85 belongs with the Bay of Fundy group or with the Northeast Channel group, and whether Stratum 60 belongs with the Shelf Basins or with the Inner Central Group.

Relative Abundance and Dominance

In the preceeding cluster and discriminant analyses species abundances were standardized so that the weight of each species would be somewhat equalised. However, in terms of numbers, the assemblages being described here are dominated by a few species only, usually those of commercial importance. This pattern of dominance has persisted over the study period (Table 7). Redfish, for example, dominate the slopes and basins, whereas haddock are dominant in the Bay of Fundy and on the Western Banks and surrounding middle depths (Outer central stratum-group).

Seasonal Differences

The species and stratum-groups resulting from the fall surveys (Figs. 5, 7, and 11) are recognizably similar to those observed in the summer surveys. In contrast, the stratum groupings from the spring surveys are far less geographically coherent, particularly for middle depth and shallow strata (Figs. 5, 7, and 9). In spring there are two 'mixed' groups of strata, and the east/west split of the banks is not as clean as in the summer and fall; Sable Island, Western, and Emerald Banks cluster with Browns Bank, rather than with Banquereau to the east; and Roseway, Lahave, and Scatarie cluster together. In the fall, just as in summer, the east-west split in the banks occurs between Sable Island and Western Banks.

The deep strata show similar groupings at all three times of year. The slope of the Laurentian Channel, the outer slope of the shelf, the Northeast channel and the shelf basins all tend to form relatively separate clusters.

Discussion and Conclusions

This study has provided a large-scale view of the distribution of assemblages of demersal fishes on the Scotian Shelf and in the Bay of Fundy. During the planning stages of the Southwest Nova Scotia Fishery Ecology Program, (FEP) (Smith et al. 1989), it was necessary to base decisions about the geographical extent of the Program on existing knowledge of single species distributions, and the physical environment. In the light of the results of this study it is possible to evaluate the extent to which the assemblages in the area chosen for the FEP differ from those in adjacent areas. As was previously known from single species analyses, it is clear that haddock are the dominant

TABLE 5. Constancy and fidelity of species groups in stratum groups for summer periods. For constancy, blank = 0, · = 0<0.25, — = 0.25<0.50, + = 0.50<0.75, * = 0.75<1.0. For fidelity, blank = 0, · = 0<0.5, — = 0.5>1.0, + = 1<2, * = >2.

	Stratum groups										
Species groups	1	2	3	4	5	6	7	8	9	10	11
Constancy											
Grenadier/longfin hake	*					*		*	·	+	+
Redfish/argentine/cusk			*		*	—	·	+	+	*	+
White hake/witch/silver hake	—	+	+	·	*	+	+	+	+	+	+
Spiny dogfish/pollock			+	·	*	·	·	·	—	*	*
Angler/smooth skate/red hake		·	*	*	*	·	·	·	*	*	·
Wolffish/halibut/haddock	*	·	·	+	+	+	·	*		*	·
Plaice/thorny skate/cod	+	+	+	+	+	+	+	—	—	+	·
Yellowtail/winter skate/longhorn	*	+	*	—	*	·	·			*	*
Little skate/sea raven/winter flounder	*	·	—	*		*					
Fidelity											
Grenadier/longfin hake	*					*		·	—	+	+
Redfish/argentine/cusk			*		*	—	—	+	+	·	+
White hake/witch/silver hake	*	—	—	*	*	—	—	—	—	—	—
Spiny dogfish/pollock			+	·	·	—	—	—	+	*	*
Angler/smooth skate/red hake		—	·	·	·	—	—	—	*	·	—
Wolffish/halibut/haddock	*	—	·	+	+	—	·	*		*	·
Plaice/thorny skate/cod	—	—	·	—	—	—	—	·	·	—	·
Yellowtail/winter skate/longhorn	*	+	·	—	*	—	—			*	·
Little skate/sea raven/winter flounder	·	+	+	*		*					

TABLE 6. Coefficients of separate determination for summer stratum groups. These show the relative importance of each variable on each axis. The eigenvalues show the relative amount of group separation accounted for by each axis.

	Discriminant axes		
Variable	Axis 1	Axis 2	Axis 3
Depth	38.1	2.4	0.1
Salinity	14.4	0.3	9.9
Temperature	6.0	71.4	7.3
SEDSIZE	17.2	18.8	51.0
SEDSORT	15.8	6.1	29.2
SEDSAND	8.5	1.0	2.6
Eigenvalues	2.3	0.6	0.2
Percent of group separation	69.6	18.6	5.1

demersal fish species in all but the deepest strata in the FEP study area. Thus, with haddock as the focal species, the choice of area was well founded.

Certain conclusions in the discussion which follows can be related specifically to the FEP study area. First, the assemblages are as heterogeneous in the FEP area as in any other area of similar size on the Scotian Shelf. Conclusions regarding the lack of clear assemblage boundaries apply in the FEP area as well as in other areas of the Scotian Shelf, and the assemblages which occur appear more related to depth than to special conditions in the general area. Functionally, given that haddock are distributed across the various assemblages in the area, it is unlikely that they are part of a highly coevolved assemblage which could be considered as an ecological entity.

Are there Distinct Demersal Fish Communities on the Scotian Shelf?

Assemblage definition is particularly problematic in marine systems which are largely "open." For demersal fishes on continental shelves this problem has most frequently been approached using cluster or similar analyses of trawl survey data. Studies in the Gulf of Guinea (Fager and Longhurst 1968), the Campeche Bank (Sauskan and Ryzhov 1977), the Pacific coast of North America (Day and Pearcy 1968; Gabriel and Tyler 1980), and Atlantic coast of North America (Wenner 1983; Colvocoresses and Musick 1984; Overholtz and Tyler 1985) report finding assemblages or species associations, usually related to the physical environment. Depth, salinity, oxygen, and substrate type are usually the measured variables.

Indeed, whether or not distinct biotic communities exist was one of the earliest debates of community ecology (Mills 1969). At one extreme is the argument that the species in assemblages are distributed independently on gradients in the physical environment, and that sharp changes in species composition correspond to sharp changes in the physical environment. At the other extreme is the view that the species comprising an assemblage are highly co-evolved, and interdependent, and that as one of the species reaches its distributional limits, the assemblage loses it integrity, giving way to another assemblage. A variation of the latter view is that structure is determined by one or a few key or cornerstone species, the absence of which results in a substantially different community.

An aim of this study was to decide if and where the assemblages of demersal fishes on the Scotian Shelf fit into the above scheme. Since most of the species groups revealed by the analysis break down from one area to another they obviously cannot be considered as 'superorganisms' in the sense that they consist of highly interdependent sets of species which cannot exist without each other. Furthermore, although there were definite changes in assemblage composition from one area to another, the changes were gradual, and no sharp assemblage boundaries were evident. Therefore, the observed patterns are more like those which would be expected from largely independent dis-

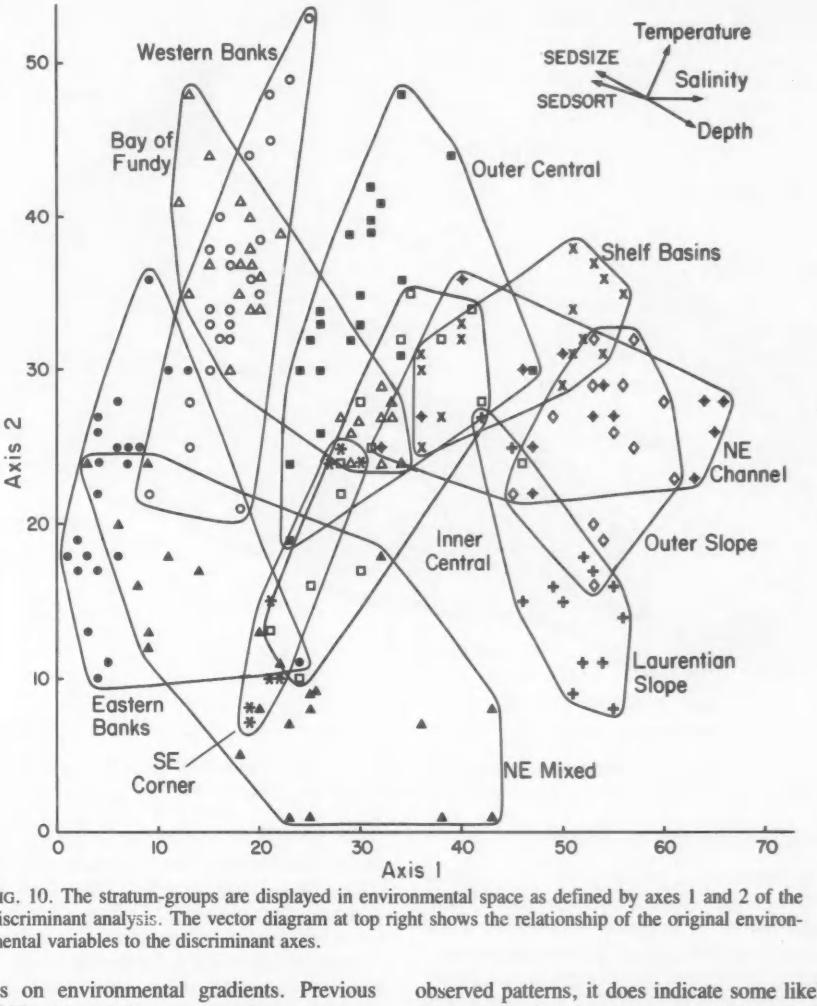

FIG. 10. The stratum-groups are displayed in environmental space as defined by axes 1 and 2 of the discriminant analysis. The vector diagram at top right shows the relationship of the original environmental variables to the discriminant axes.

tribution of species on environmental gradients. Previous studies by Scott (1982a, b) and the correspondence between environment and fish assemblages which is evident from our discriminant analysis indicate that the most important variable is depth, which is correlated with salinity and sediment type (Table 6, Fig. 10).

Most other studies on assemblages of demersal fishes on continental shelves have considered the groupings produced by the various clustering techniques as though they were discrete units (Gabriel and Tyler 1980; Wenner 1983; Overholtz and Tyler 1985). In contrast, for mesopelagic fishes off eastern Canada, McKelvie (1985) concluded that although there were faunal groups, the results were more consistent with a gradation between faunas than with abrupt change. This study results in similar conclusions for the demersal fish assemblages of the Scotian Shelf area. However, in all cases the conclusions are subjective, as rigorous tests of the randomness of species distributions on environmental gradients have not been performed.

Species Interactions

Although our analysis does not permit conclusions about the extent to which species interactions might contribute to the observed patterns, it does indicate some likely candidates for future study. As a first approach with the existing data, methods which first account for environmental effects could be attempted (e.g. Rosenzweig et al. 1984).

Two species groups with similar composition which show complementary distributions on the Eastern Banks and in the Bay of Fundy, are yellowtail/winter skate/longhorn and winter flounder/little skate/sea raven, respectively. These groups are analogous in that they are each comprised of a flatfish, a skate, and a sculpin. The ecological similarity of the flatfishes and skates in these species pairs has been previously noted (Langton and Bowman 1981; and McEachern and Musick 1975).

At a crude level, habitat partitioning would be expected within groups of ecologically similar species. In the absence of details on feeding, it is necessary to rely on taxonomic relatedness and morphology as indices of ecological similarity. In general the even distribution of the flatfishes (with the exception of halibut) and skates among the species groups (Fig. 4) suggests habitat partitioning. Although taxonomically similar, the gadids (cod, cusk, haddock, and the hakes) show sufficient morphological diversity that habitat partitioning need not be expected.

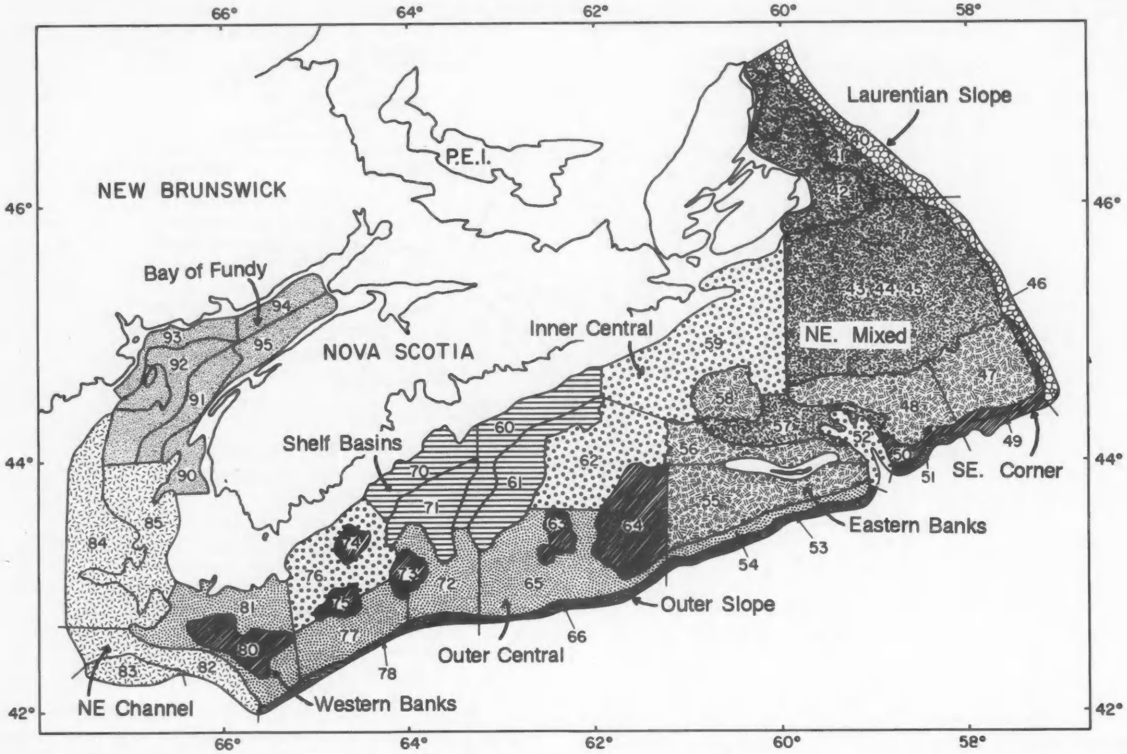

FIG. 11. Summary of the spatial pattern of demersal assemblages on the Scotian Shelf and in the Bay of Fundy based on clustering of strata and species during summer from 1970–81. Stratum-group names correspond to those in Figs. 8 and 10.

Spatial and Temporal Persistence of Assemblages

Whether or not the species and stratum-groups described in this study represent functionally distinct communities, it is clear that there is a high degree of temporal persistence of the observed patterns at the spatial scale of a sampling stratum. Ideally, studies of the persistence of assemblages should extend over at least one full turnover of individuals (Connel and Sousa 1983). The life spans of the fishes in this study vary considerably from a few years for species such as mailed sculpin, argentine, sand lance, or silver hake, to greater than 50 yr for the redfishes. Among the commercially important gadids, longevity would be in the range of 10–16 yr, whereas for the flatfishes 15–30 yr would be common. However, at the high fishing mortality rates experienced by these populations individuals approaching the maximum possible age are seldom found. For example, in 1978, the mean age of haddock (longevity 16 yr) from the eastern Scotian Shelf was 2.1 yr (Mahon et al. 1985). Consequently, in a situation such as this, 50% turnover time might be a more appropriate consideration than longevity. For the majority of species on the Scotian Shelf 50% turnover would be expected in 3–10 yr. Therefore, it is unlikely that the apparent persistence of assemblage structure is due to the dominance of a few good year classes over the period in question.

Connell and Sousa (1983) point out the difficulty of evaluating persistence and stability of exploited populations or assemblages, since the mortality due to harvesting is seldom known. In the Northwest Atlantic, the fisheries for the dominant species are well documented. The trends, from the early 1950s through the mid 1970s, have been similar for most continental shelf areas of the Northwest Atlantic (Brown and Halliday 1983). There have been substantial declines in biomass of most finfish resources. As Brown and Halliday (1983) point out, it is impossible to be certain about the causes of the declines of these species which led to the low levels of abundance in the late 1960s and early 1970s. However, they did follow closely on a period of high mortality due to exploitation by large distant water fleets. Considering that the recovery, in the late 1970s, of the biomass of the main commercially exploited species, followed the regulated reduction of fishing mortality, Brown and Halliday (1983) conclude that the fluctuations evident in Fig. 2 were due to extreme exploitation.

It is evident that the surveys cover a dynamic period as regards biomass of the dominant species. The persistence of assemblage structure during the study period is even more striking in the face of the extreme perturbation due to overexploitation and depletion of many of the dominant species (Brown and Halliday 1983; Fig. 2). However, because the stocks were already depleted by the time the surveys were initiated, it is not possible to assess the extent to which the assemblage patterns may have changed prior to the surveys.

The persistence of demersal fish assemblages on the Scotian Shelf is consistent with other studies of temperate and sub-temperate demersal assemblages, primarily on the east coast of North America, but also in the North Sea (Ursin 1982). In the Middle Atlantic Bight, species associations and faunal zones were considered to be consistent over the 9-yr period (1967–76), despite strong seasonal changes in distribution in response

TABLE 7. Percent numerical contribution of each species in each stratum group over the four periods (blanks are<0.5%). Sets in which a species contributed >10% in any period are underlined to indicate a dominant species.

	Northeast Mixed				Eastern Banks				Bay of Fundy				Western Banks				Southeast Corner				Outer Central				Inner Central				Shelf Basins				Northeast channel and Adjacent Basins				Laurentian Slope				Outer Slope			
Grenadier																																		1			1	1	1	1	1	1		1
Longfin hake	1																																			1	7	4	3	3	10	16	2	20
Redfish	16	21	27	10					8	12	11	2	1				17	3	15	1	1	3	6		64	33	37	6	86	86	80	36	40	30	19	25	81	65	83	74	69	48	69	47
Argentine																				1	2	5	11	9				4			1	4	12	3	40	11					6	4	5	5
Cusk									1		1										1	1	1	1									1	2	1	2								
White hake			2						6	14	8	2								3	1	1	2	1	1	1	2	2	1		1	2	10	16	4	7	3	9	5	12	3	3	3	3
Witch flounder	2	3	1	1		1	1		4	4	4	1		1	1		3	2	3	4	1	1		1	1	2	3	4		1		1	1	1	1	2	5	16	3	3		1	2	1
Silver hake					2	1	1	8	2	2	2	1	4	3	1			1	1	1	9	31	16	15	14	20	4	31	10	10	8	44	10	17	12	12			2	1	7	18	4	10
Spiny dogfish									19	9	6	2	1			18					29		15	9					1				13	14	2	4								
Pollock									5	1	2	2			2					7	3	3	1	1		1	1	7	1		3	6	4	3	8	9								2
Vahl's eelpout		3		2																						2																		
Eelpouts	2	1	1																							1																		
Sand lance	43	6			43	1	5	1						1			6																											
Angler														1						1				1			1															1	1	1
Smooth skate	1			1					2	1	2						2	4	3	2		1	1										1	1	1	2						1	2	1
Red hake																								1			1	3				1				1							2	
Wolffish			1	1									2	2	1	1		1	1	1	1	1																						
Halibut													1	1	2				1	3																								1
Haddock			3	1	2	1	8	19	14	17	27	57	51	43	69	65	7	1	2	9	27	35	34	45	3	3	26	19			4	4	3	3	5	14							1	
Ocean pout									2	2	2	1																							1								1	
Plaice	19	44	37	50	11	11	11	16	5	4	3	2	6	4	2	1	40	57	44	38	10	7	3	6	9	20	16	17		1	1	2	2	3	1	2	1	1	2	1	2	5	5	3
Thorny skate	2	5	3	5	2	8	5	5	6	5	5	2	4	3	2	1	13	20	14	12	2	3	2	2	1	1	1	1					1	2	2	3		1	1			2	3	2
Cod	13	12	23	28	5	22	13	17	10	8	12	10	11	13	8	7	6	5	4	13	5	3	3	4	5	13	5	4					1	2	2	3		2		4				2
Barndoor skate																			1																									
Mailed sculpin		1											1	1			1			1																								
Yellowtail flounder			1		28	44	46	28					11	19	8	4	3	3	13	2	5	1	2	4			1	1															1	
Winter skate						1	1	2		1	1	1	1	1																														
Longhorn sculpin					4	8	7	3	7	11	5	4	3	5	2	1					1	2	1													1								
Little skate									1	1	1																																	
Sea Raven						1			4	2	3	3	1																															
Winter flounder					1	1			2	3	4	7																																
Period	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4

to changes in temperature (Colvocoresses and Musick 1983; Musick et al. 1985). The faunal groups were arranged on temperature and depth gradients, with temperature being the dominant environmental factor determining fish distributions. Similarly, Overholtz and Tyler (1985) found persistent assemblages in the area of Georges Bank; however, these were arranged primarily on a depth/salinity gradient.

Since these assemblages have all been heavily exploited for decades, one can conclude that they are stable when perturbed and persistent. In contrast, tropical demersal assemblages appear to change more drastically when exploited (Pauly 1979), but there is no information on persistence of such assemblages in an unexploited state. Therefore, although it appears reasonable to conclude that they are unstable, they may well be persistent in the absence of perturbation.

Other studies have found considerable variability in persistence and stability among fish assemblages and habitats. Koslow et al. (1988). found that reef fish assemblages changed substantially under exploitation. However, the picture is far from clear regarding the persistence of reef fish assemblages under natural conditions (Anderson et al. 1981; Ogden and Ebersole 1981; Galzin 1987; Sale 1980). Tidepool fish assemblages appear to be persistent and resilient (Thompson and Lehner 1976; Grossman 1982; Collette 1986), possibly due to the relatively low number of species capable of inhabiting them. In rivers and streams, persistence and stability appear to vary with stream type. Salmonid assemblages in cold streams appear to be more persistent and stable than assemblages in warmwater streams, where diversity is higher (Grossman et al. 1982; Moyle and Vondracek 1985).

Our conclusions are consistent with the general pattern which is emerging for fish assemblages. The pattern is one of simple assemblages in homogeneous habitats being more stable when perturbed, and possibly also more persistent in the absence of perturbation, than diverse assemblages in heterogeneous habitats. Although the pattern is becoming clearer, the theoretical basis for predicting where a particular type of assemblage will lie on the persistence/stability scale is not yet established (Sugihara et al. 1984). The fact that many of these assemblages are exploited is a complicating factor. For most assemblages, exploitation is likely to be a qualitatively different type of perturbation from others to which the assemblage will have been exposed on an evolutionary time-scale.

Implications for Multispecies Management

Any kind of 'multispecies' strategy will need to consider the question of management units. Many factors (e.g. species distributional patterns, fleet fishing patterns, practicalities of monitoring and surveillance) will influence the definition of management units. Here, in the context of a scheme based on 'assemblage regions' and 'assemblage production units' (Tyler et al. 1981), we consider the relevance of the present study to defining management units.

Assemblage regions are defined as geographical areas of relatively consistent species composition within which there may be one or more assemblage production units (APUs), i.e. trophically linked groups of species. By analogy to the single species approach, an APU would be similar to a species, whereas an assemblage region would be similar to stock management area. The basic assumption is that these units would be more functionally discrete than single species. Tyler et al. (1981) suggest that cluster analysis would be a valid way of defining assemblage regions and APUs.

Taking the results of the present analysis at face value, the stratum-groups could be interpreted as corresponding to assemblage regions and the species groups as corresponding to APUs. The two-way table shows which species groups are most prominent in each stratum-group (Fig. 6). Because the pattern appears to be temporally persistent it will at least be useful in dealing with technological interactions. However, if it is to be useful in dealing with species interactions (predation, competition) then the dynamics of the units described must be predictable or 'better behaved' than the individual elements comprising them. This analysis is, therefore, only a basis for the further study of the dynamics of these units.

At this stage, there is insufficient information on feeding to assess whether the species groups defined here have any functional significance in an ecological sense. The members of a group could simply be responding to the physical environment in the same way.

In conclusion it appears that there is a persistent spatial pattern of groundfish distribution on the Scotian Shelf. This pattern appears to be strongly influenced by the physical environment, perhaps much more so than by species interactions. The existence of regions which are relatively homogeneous with regard to species composition can be useful in dealing with bycatch problems (Brodie 1985; Murawski et al. 1983; Sinclair 1985). However, we are at a very early stage as regards defining ecologically based management units in the area, if indeed these exist.

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The data analysed here represent 12 yr of diligent attention to detail on the part of a large number of individuals at the Marine Fish Division. No sense of this is conveyed in the technical descriptions of the more than 36 cruises, and the subsequent coding, editing, and custodianship of the resulting data. Only here can we attempt to convey our admiration for the foresight of the scientists who planned this survey time-series, and for the dedication of the people who actually collected these data and brought it to the point where we could carry out this analysis. We also thank several individuals who were directly involved in the preparation of this paper. Dr. James Scott provided his ideas and encouragement freely. Reviews by Drs. Don Waldron, Ian Perry, and Brock Bernstein played a significant role in improving the manuscript.

References

Anderson, G. R. J., A. H. Ehrlich, P. R. Ehrlich, J. D. Roughgarden, B. C. Russell, and F. H. Talbot. 1981. The community structure of coral reef fishes. Am. Nat. 117: 476–495.

Anderson, K. P., and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorous circulation and primary production. Meddr. Danm. Fisk.-og Havunders 7: 319–435.

Austin, M. P., and L. Belbin. 1982. A new approach to the inverse classification problem in floristic analysis. Aust. J. Ecol. 7:75–89.

Baker, J. A., and S. T. Ross. 1981. Spatial and temporal resource utilization by southeastern cyprinids. Copeia 1981: 178–189.

Barbour, C. B., and J. H. Brown. 1974. Fish species diversity in lakes. Am. Nat. 108: 473–489.

Bernstein, B. B., R. R. Hessler, R. Smith, and P. A. Jumars. 1978. Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. Limnol. Oceanogr. 23: 401–416.

Bigelow, H. B. 1927. Physical oceanography of the Gulf of Maine. U.S. Dep. Commer. Bur. Fish. Bull. 40: 511–1027.

Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. U.S. Environmental Protection Agency, Ecological Research Series EPA-600/3-77-033.

Brodie, W. B. 1985. Review of methods and data used in analysing multispecies fisheries interactions, p. 55–59. *In* R. Mahon [ed.] Towards the inclusion of fishery interactions in management advice. Can. Tech. Rep. Fish. Aquat. Sci. No. 1347.

Brown, B. E., and R. G. Halliday. 1983. Fisheries resources of the northwest Atlantic — some responses to extreme fishing perturbation. Proc. Joint Oceanographic Assembly 1982 — General Symposia. Canadian National Committee/Scientific Committee on Oceanic Research, Ottawa. 96–109.

Campana, S., and J. Simon. 1986. Assessment of the 4X cod fishery in 1985. CAFSAC Res. Doc. 86/35: 55 p.

Clifford, H. T., and W. Stephenson. 1975. An introduction to numerical classification. Academic Press. 229 p.

Collette, B. B. 1986. Resilience of the fish assemblage in New England tidepools. Fish. Bull. 84: 200–204.

Colvocoresses, J. A., and J. A. Musick. 1984. Species associations and community composition of Middle Atlantic Bight continental shelf demersal fishes. Fish. Bull. 82: 295–313.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. Am. Nat. 121: 789–824.

Cooley, W. A., and P. R. Lohnes. 1971. Multivariate data analysis. John Wiley and Sons, New York. 364 p.

Day, D. A., and W. G. Pearcy. 1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. J. Fish. Res. Board Can. 25: 2665–2675.

Doubleday, W. G. [ed]. 1981. Manual on groundfish surveys in the Northwest Atlantic. NAFO Sci. Coun. Studies 2: 55 p.

Drapeau, G. and L. H. King. 1971. Surficial geology of Yarmouth-Browns Bank map area. Geol. Surv. Can. Pap. 72-24. 6 p.

Fader, G. B., L. H. King, and H. W. Josenhans. 1982. Surficial geology of the Laurential Channel and the western Grand Banks of Newfoundland. Geol. Surv. Can. Pap. 81-82. 37 p.

Fader, G. B., L. H. King, and B. MacLean. 1977. Surficial geology of the eastern Gulf of Maine and Bay of Fundy. Geol. Surv. Can. Pap. 76-17. 23 p.

Fager, E. W., and A. R. Longhurst. 1968. Recurrent group analysis of species assemblages of demersal fish in the Gulf of Guinea. J. Fish. Res. Board Can. 25: 1405–1421.

Gabriel, W. L., and S. A. Murawski. 1985. The use of cluster analysis in identification and description of multispecies systems, p. 112–117. *In* R. Mahon [ed.] Towards the inclusion of fishery interactions in management advice. Can. Tech. Rep. Fish. Aquat. Sci. No. 1347.

Gabriel, W.L., and A.V. Tyler. 1980. Preliminary analysis of Pacific coast demersal fish assemblages. Mar. Fish. Rev. 1980: 83–88.

Gladfelter, W. B., J. C. Ogden, and E. H. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61: 1156–1168.

Gorman, O. T., and T. R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59: 507–515.

Green, R. H., and G. L. Vascotta. 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. Water Res. 12: 583–590.

Grossman, G. D. 1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. Am. Nat. 119: 611–637.

Grossman, G. D., P. B. Moyle, and J. O. Whittaker, Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Am. Nat. 120: 423–454.

Halliday, R. G., and W. G. Doubleday. 1976. Catch and effort trends for the finfish resources of the Scotian Shelf and estimates of the maximum sustainable yield of groundfish (except silver hake). ICNAF Sel. Pap. 1: 117–128.

Halliday, R. G., and P. A. Koeller. 1981. A history of Canadian ground fish trawling surveys and data usage in ICNAF Divisions 4TVWX. Can. Spec. Publ. Fish. Aquat. Sci. 58: 27–41.

Heezen, B. C., M. Tharp, and M. Ewing. 1959. The floors of the oceans: Part 1, the North Atlantic. Geol. Soc. Amer. Spec. Pap. 65: 122 p.

Herbold, B. 1984. Structure of an Indiana stream fish association: choosing an appropriate model. Am. Nat. 124: 561–572.

Hobson, E. S., and W. H. Lenarz. 1977. Report of a colloquium on the multispecies problem, June 1976. Mar. Fish. Rev. 39(9): 8–13.

Horwitz, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. Ecol. Monogr. 48: 307–321.

Hope, K. 1969. Methods of multivariate analysis. Gordon and Breach, Publ., N.Y. 288 p.

Houghton, R. W., P. C. Smith, and R.O. Fournier. 1978. A simple model for cross-shelf mixing on the Scotian Shelf. J. Fish. Res. Board Can. 325: 414-421.

King, L. H. 1967. Use of a conventional echo sounder and textural analyses in delineating sedimentary facies. Can. J. Earth Sci. 4: 691—708.

1970. Surficial geology of the Halifax–Sable Island map area. Mar. Sci. Pap. 1: 16 p.

Koslow, J. A., F. Hanley, and R. Wicklund. 1988. Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. Mar. Ecol. Prog. Ser. 43: 201–212.

Lance, G. N., and W. T. Williams. 1967. A general theory of classificatory sorting strategies. I. Hierarchical systems. Computer J. 9: 373–380.

Langton, R. W., and R. E. Bowman. 1981. Food of eight northwest Atlantic pleuronectiform fishes. NOAA Tech. Rep. NMFS SSRF-749: 16 p.

MacLean, B., G. B. Fader, and L. H. King. 1977. Surfical geology of Canso Bank and adjacent areas. Geol. Surv. Can. Pap. 76-15. 11 p.

MacLean, B., and L. H. King. 1971. Surficial geology of the Banquereau and Misaine Bank map area. Geol. Surv. Can. Pap. 71-22. 19 p.

Mahon, R. 1984. Divergent structure in fish taxocenes of north temperate streams. Can. J. Fish. Aquat. Sci. 41: 330–350.

Mahon, R., P. Simpson, and D. E. Waldron. 1985. The eastern Scotian Shelf haddock fishery in 1984, with an historical perspective on stock and recruitment back to 1949. CAFSAC Res. Doc. 85/47: 64 p.

Mahon, R., and R. W. Smith. 1989. Comparison of species composition in a bottom trawl calibration experiment. J. Northwest Atl. Fish. (In press).

Mahon, R., R.W. Smith, B.B. Bernstein, and J.S. Scott. 1984. Spatial and temporal patterns of groundfish distribution on the Scotian Shelf and in the Bay of Fundy, 1970–1981. Can. Tech. Rep. Fish. Aquat. Sci. No. 1300: 164 p.

McEachran, J. D., and J. A. Musick. 1975. Distribution and relative abundance of seven species of skates (Pisces: Rajidae) which occur between Nova Scotia and Cape Hatteras. Fish. Bull. 73: 110–136.

McGlade, J., M. C. Annand, B. Beanlands, and A. F. Sinclair. 1986. Assessment of Division 4VWX and Subarea 5 pollock (*Pollachius virens*). CAFSAC Res. Doc. 86/118: 45 p.

McKelvie, D. S. 1985. Discreteness of pelagic faunal regions. Mar. Biol. 88: 125–133.

Mendelson, J. 1975. Feeding relationships among species of *Notropis* (Pisces: Cyprinidae) in a Wisconsin stream. Ecol. Monogr. 45: 119–230.

Mercer, M. C. [ed.] 1982. Multispecies approaches to management advice: workshop report. Can. Spec. Publ. Fish. Aquat. Sci. 59: 1–15.

Mills, E. L. 1969. The community concept in marine zoology, with comments on continua and instability in some communities: a review. J. Fish. Res. Board Can. 26: 1415–1428.

Moyle, P. B., and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology 66: 1–13.

Murawski, A. W. 1983. Mixed species yield-per-recruitment analysis accounting for technological interactions. Can. J. Fish. Aquat. Sci. 41: 897–916.

Murawski, S. A., and J. T. Finn. 1988. Biological bases for mixed species fisheries: species co-distribution in relation to environmental and biotic variables. Can. J. Fish. Aquat. Sci. 45: 1720–1735.

Murawski, S. A., A. M. Lange, M. P. Sissenwine, and R. K. Mayo. 1983. Definition and analysis of multispecies otter-trawl fisheries off the northeastern coast of the United States. J. Cons. Int. Explor. Mer 41.

Musick. J. A., J. A. Colvocoresses, and E. J. Foell. 1985. Seasonality and the distribution, availability and composition of fish assemblages in Chesapeake Bight, p. 451–474. *In* A. Yanez Arancibia [ed.] Fish community ecology in estuaries and coastal lagoons; towards an ecosystem integration. DR (R) UNAM Press, Mexico.

O'Boyle, R., and R. Gregory. 1985. An evaluation of the population dynamics of 4X haddock during 1962–84 with yield projected to 1986. CAFSAC Res. Doc. 85/109: 81 p.

Ogden, J. C., and J. P. Ebersole. 1981. Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. Mar. Ecol. Prog. Ser. 4: 97–103.

Overholtz, W. J., and A. V. Tyler. 1985. Long-term responses of the demersal fish assemblages of Georges Bank. Fish. Bull. 83: 507—520.

Pauly, D. 1979. Theory and management of tropical multispecies stocks. ICLARM Studies and Reviews No. 1: 35 p.

Rahel, R. J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. Ecology 65: 1276–1289.

Rahel, F. J., J. D. Lyons, and P. A. Cochran. 1984. Stochastic or deterministic regulation of assemblage structure, it may depend on how the assemblage is defined. Am. Nat. 124: 583–589.

Rosenzweig, M. L., Z. Abramsky, and S. Brand. 1984. Estimating species interactions in heterogeneous environments. Oikos 43: 329–340.

SALE, P. 1977. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111: 337–359.

1980. Assemblages of fish on patch reefs – predictable and unpredictable. Environ. Biol. Fish. 5: 243–249.

SAUSKAN, V. I., AND V. M. RYZHOV. 1977. Investigation of communities of demersal fish of Campeche Bank. Oceanology 17: 223–227.

SCOTT, J. S. 1981. Summer distribution of groundfishes on the Scotian Shelf, p. 181–193. *In* W.G. Doubleday and D. Rivard [ed.] Bottom trawl surveys. Can. Spec. Publ. Fish. Aquat. Sci. No. 58.

1982a. Selection of bottom type by groundfishes of the Scotian Shelf. Can. J. Fish. Aquat. Sci. 39: 943–947.

1982b. Depth, temperature, and salinity preferences of common fishes on the Scotian Shelf. J. Northw. Atl. Fish. Sci. 3: 39–39.

SINCLAIR, A. F. 1985. A linear programming analysis of Scotian Shelf offshore fisheries, p. 92–102. *In* R. Mahon [ed.] Towards the inclusion of fishery interactions in management advice. Can. Tech. Rep. Fish. Aquat. Sci. No. 1347.

SINCLAIR, A. F., AND S. GAVARIS. 1985. Sequential population analysis of 4VsW cod following the 1984 fishery. CAFSAC Res. Doc. 85/48: 28 p.

SINCLAIR, M., J. J. MAGUIRE, P. KOELLER, AND J. S. SCOTT. 1984. Trophic dynamic models in light of current resource inventory data and stock assessment results. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 183: 269–284.

SMITH, P. C. 1983. The mean and seasonal circulation off southwest Nova Scotia. J. Phys. Ocean 13: 1034–1054.

SMITH, P. C., K. T. FRANK, AND R. MAHON 1989. Introduction to Southwest Nova Scotia Fisheries Ecology Program: 1982–89. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): (This issue).

SMITH, R. W. 1976. Numerical analysis of ecological survey data. Ph.D. thesis, Univ. of S. Calif., Los Angeles. 401 p.

SMITH, R. W., B. B. BERNSTEIN, AND R. L. CIMBERG. 1988. Community environmental relationships in the benthos: applications of multivariate analytical techniques, p. 247–326. *In* Marine organisms as indicators. Springer-Verlag, New York, NY.

STEPHENSON, W., W. T. WILLIAMS, AND S. D. COOK. 1972. Computer analyses of Petersen's original data on bottom communities. Ecol. Monogr. 42:387–415.

STULL, J. K., C. I. HAYDOCK, R. W. SMITH, AND D. E. MONTAGNE. 1986. Long-term changes in the benthic community on the coastal shelf of Palos Verdes, Southern California. Mar. Biol. 91: 539–551.

SUGIHARA, G., S. GARCIA, J. A. GULLAND, J. H. LAWTON, H. MASKE, R. T. PAINE, T. PLATT, E. RACHOR, B. J. ROTHSCHILD, E. A. URSIN, AND B. F. K. ZEITZSCHEL. 1984. Ecosystem Dynamics Group Report, p. 131–153. *In* R. M. May [ed.]. Exploitation of marine communities. Dahlem Konferenzen 1984. Springer-Verlag, New York.

SUTCLIFFE, W. H., JR., R. H. LOUCKS, AND K. F. DRINKWATER. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and Gulf of Maine. J. Fish Res. Board Can. 33: 98–115.

THOMPSON, D. A., AND C. E. LEHNER. 1976. Resilience of a rocky intertidal fish community in a physically unstable environment. J. Exp. Mar. Biol. Ecol. 22: 1–29.

TRITES, R. W., AND R. H. LOUCKS. 1985. Environment on the east coast and in particular the Scotian Shelf, p. 163–182. *In* R. Mahon [ed.] Toward the inclusion of fishery interactions in management advice. Can. Tech. Rep. Fish. Aquat. Sci. No. 1347.

TYLER, A. V., W. L. GABRIEL, AND W. J. OVERHOLTZ. 1982. Adaptive management based on structure of fish assemblages of northern continental shelves. Can. Spec. Publ. Fish. 59: 149–156.

UCHUPI, E. 1968. Atlantic continental shelf and slope of the United States — physiography. Geol. Surv. Pref. Rap. 529-C. 30 p.

WENNER, C. A. 1983. Species associations and day/night variability of trawl caught fishes from the inshore sponge-coral habitat, South Atlantic Bight. Fish. Bull. 81: 537–552.

WERNER, E. E. D. J. HALL, D. R. LAUGHLIN, D. J. WAGNER, L. A. WILSMAN, AND F. C. FUNK. 1977. Habitat partitioning in a freshwater fish community. J. Fish. Res. Board Can. 34: 360–370.

WIENS, J. A. 1981. Single-sample survey of communities: are the revealed patterns real? Am. Nat. 117: 90–98.

Reproductive Biology of Southwest Scotian Shelf Haddock (*Melanogrammus aeglefinus*)[1]

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Information on the reproductive biology of Southwest Scotian Shelf haddock (*Melanogrammus aeglefinus*) (NAFO Division 4X) is presented including geographic distribution by maturation stage, timing of maturation, seasonal changes in gonad weight, spawning distribution in relation to environmental factors, and fecundity at length, weight, and age. Haddock were found to spawn on Browns, Baccaro, LaHave, and Roseway Banks over sand/gravel substrates. Spawning fish were found in a narrower and colder temperature range than were fish of other maturity stages. Spawning fish were found from April to August with peak activity occurring from April to June. Testes peaked in weight in February and March when they accounted for 1–2.2% of body weight while ovaries reached their maximum size (3.1–12.5% of body weight) from late March to mid-May. The length at 50% maturity varied over the period 1970–85 and these changes were correlated with changes in population biomass. There were no significant differences in fecundity/length relationships with area or year (1983–86) but fecundity for a given size decreased over the spawning season.

Présentation de données sur la biologie de la reproduction de l'aiglefin (*Melanogrammus aeglefinus*) du sud-ouest du plateau Scotian (Division 4X de l'OPANO), notamment sur la distribution géographique par stade de maturation, la chronologie de la maturation, les changements saisonniers du poids gonadique, la distribution du frai en relation avec les facteurs environnementaux et la fécondité en fonction de la longueur, du poids et de l'âge. Il est apparu que l'aiglefin se reproduisait sur les bancs Browns, Baccaro, LaHave et Roseway sur des substrats de sable et de gravier. Les poissons en reproduction ont été observés dans une gamme de températures plus étroite et plus basse que les poissons à d'autres stades de maturation. Les poissons en reproduction ont été observés d'avril à août, l'activité atteignant un sommet entre avril et juin. Les testicules atteignaient leur poids le plus élevé en février et en mars, moment où ils représentaient de 1 à 2.2 % du poids corporel, tandis que les ovaires atteignaient leur taille maximale (3.1–12.5 % du poids corporel) entre la fin mars et la mi-mai. La longueur au stade 50 % de maturité variait dans la période de 1970 à 1985 et ces changements ont été correliés aux changements dans la biomasse de la population. Aucune différence importante n'a été observée dans le rapport fécondité/longueur selon la région ou l'année (1983–86), mais la fécondité pour une taille donnée décroissait à mesure que se prolongeait la saison du frai.

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Research on the reproductive biology of haddock (*Melanogrammus aeglefinus*) is extensive and includes studies on the egg maturation cycle (Robb 1982), bioenergetics (Hislop et al. 1978), factors affecting fecundity (Hodder 1963, 1965; Sonina 1973; Hislop and Shanks 1979; Alekseyeva and Tormosova 1980), and spawning behaviour (Hawkins et al. 1967). Changes in reproductive parameters in response to environmental factors (Hodder 1965), exploitation pressure and population density (Templeman et al. 1978; Templeman and Bishop 1979) are well known. Such knowledge is generally considered prerequisite to an understanding of population dynamics, recruitment mechanisms, and stock structure, and is essential for fisheries management.

Despite its socio-economic importance, relatively little work has been done on the reproductive biology of the Southwest Scotian Shelf (NAFO Division 4X) haddock stock. Exceptions include the earlier studies on inshore stocks by Homans and Vladykov (1954); and Kohler (1959). More recently, Scott (1983) conducted a preliminary analysis of the inferred spawning areas and Beacham (1983) presented an analysis of size and age at sexual maturation of several haddock stocks including the 4X population.

In the following study, we examine the reproductive biology of Southwest Scotian Shelf haddock including distribution by maturity stage, the influence of environmental factors on distribution of spawning, timing of spawning, maturation, gonad weight/body weight relationships, length at maturity, and fecundity.

Materials and Methods

The 38 cruises involved in the subsequent analyses (Table 1) fall into four main categories: 13 summer groundfish surveys (1970–83), based on a stratified random design; nine dedicated spring cruises (1970–72, 1974–79) based on a fixed station design; 12 spring and fall surveys based on a stratified random

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[1] Fisheries Ecology Program Contribution Number: 18.

TABLE 1. Details of cruises used in analyses. Cruise codes are as follows: A = *A.T. Cameron*, H = *Lady Hammond*, N = *Alfred Needler*. Analysis codes are: M = length at maturity, seasonal variation in maturity; T = spawning temperature, depth, salinity; F = fecundity and gonad/body weight relationships, D = distribution. Sp, Su, and Fa are Spring, Summer, and Fall cruises, respectively.

Year	Cruise	Date	Season	Analysis
1970	A170	13/03 – 22/03	Sp	M,T,D
1970	A175	06/07 – 16/07	Su	M,,D
1971	A184	19/03 – 31/03	Sp	M,T,D
1971	A188	29/06 – 09/07	Su	M,D
1972	A196	04/03 – 11/03	Sp	M,T,D
1973	A212	09/07 – 20/07	Su	M,,D
1974	A219	05/03 – 14/03	Sp	M,T,D
1974	A225	09/07 – 19/07	Su	M,,D
1975	A232	15/02 – 22/02	Sp	M,T,D
1976	A243	20/02 – 28/02	Sp	M,T,D
1976	A250	12/07 – 22/07	Su	M,,D
1977	A259	21/03 – 31/03	Sp	M,T,D
1977	A265	09/07 – 20/07	Su	M,,D
1978	A274	11/03 – 20/03	Sp	M,T,D
1979	A288	21/03 – 31/03	Sp	M,T,D
1979	A292	06/07 – 16/07	Su	M,,D
1979	H027	29/10 – 08/11	Fa	M
1980	H034	17/03 – 27/03	Sp	M,T,D
1980	H037	07/07 – 15/07	Su	M,,D
1980	A306	07/07 – 15/07	Su	M,,D
1980	H042	03/09 – 10/10	Fa	M
1981	H049	09/03 – 19/03	Sp	MD
1981	H059	04/07 – 12/07	Su	M,,D
1981	H065	13/10 – 22/10	Fa	M
1982	H072	16/03 – 24/03	Sp	M,T,D
1982	H080	09/07 – 19/07	Su	M,,D
1982	H085	12/10 – 26/10	Fa	M
1983	H088	06/01 – 18/01	Sp	M,T,D,F
1983	H095	04/05 – 15/05	Sp	M,T,D,F
1983	N010	25/05 – 04/06	Sp	M,T,D,F
1983	H101	08/07 – 14/07	Su	M,,D
1983	N012	05/07 – 15/07	Su	M,,D
1983	N015	30/08 – 06/09	Fa	M
1983	N018	17/10 – 27/10	Fa	M
1984	N025	17/03 – 27/03	Sp	M,T,D,F
1984	N037	22/10 – 02/11	Fa	M
1985	N041	28/02 – 08/03	Sp	M,T,D,F
1986	N059	03/03 – 13/03	Sp	F

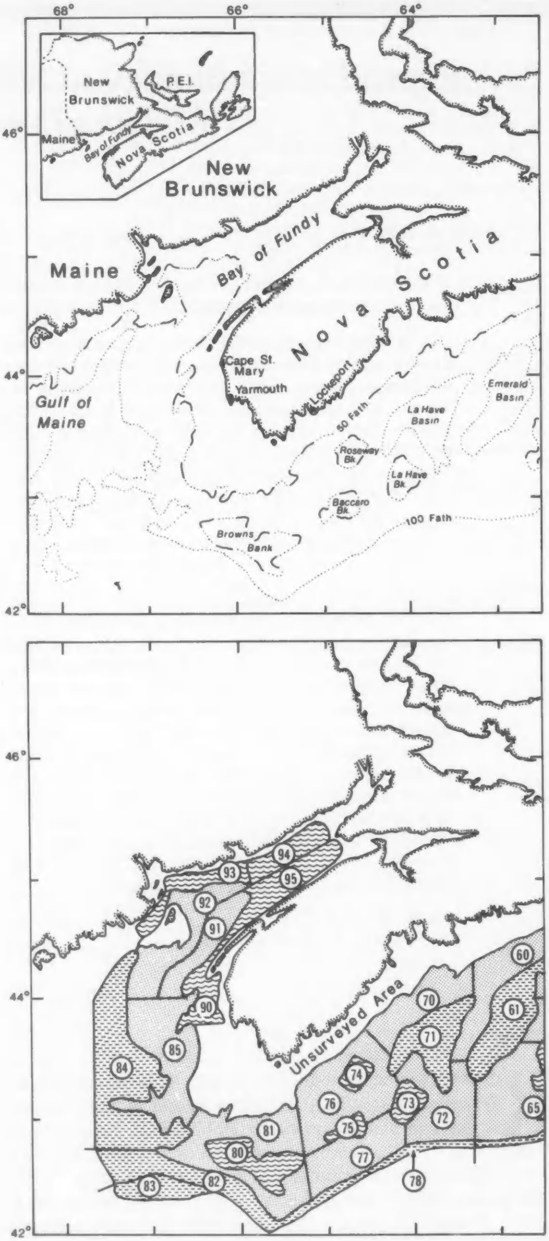


FIG. 1. Maps of Southwest Scotian Shelf showing major features (upper panel). Unsurveyed areas and survey stratum boundaries (and numbers) are indicated in the lower panel.

design (1979–85) and three dedicated seasonal surveys (1983), based on a stratified random design. Fecundity samples were collected on one additional spring cruise in 1986. Details of the survey gears and methods are given in Halliday and Koeller (1981). The stratification scheme and the areas not covered due to untrawlable bottom, are illustrated in Fig. 1. Individual fork lengths (± 1 cm), weights (± 12.5 g), sex, and maturity stages were recorded from length-stratified samples. Length frequencies were tallied for each set. Bottom temperatures (±0.1°C) and salinities (±0.005 ppt) were determined from reversing bottle casts.

Maturity stages were assigned at sea based on gross morphological characteristics, hence the criteria used were less refined than those developed on the basis of histological examination (Robb 1982; Alekseyeva and Tormosova 1980). The criteria used to define categories (Table 2) originated from Homans and Vladykov (1954) but were modified and amalgamated with the classification for Atlantic cod (*Gadus morhua*) devised by Powles (1958). Stages 1 to 6 from the Homans and Vladykov (1954) study are referred to, respectively as: resting, ripening 1 (R1), ripening 2 (R2), ripe, spawning (or running), and spent. Two other categories were also used — immature for fish which had not spawned previously and recovering, an intermediate stage between spent and resting. In 1970, Halliday and Livingstone (R. G. Halliday, pers. comm.) clarified the

TABLE 2. Definition of maturity stages for haddock used in this study (from Gavaris 1988).

		Female	Male
Stage I	Immature (Imm)	Ovaries small and firm; pale pink or reddish and somewhat transparent.	Testes slender; appear as a clear, crimped, and slender string.
Stage II	Ripening 1 (R1)	Ovaries slightly larger than in Stage I but still small and firm; contains microscopic, yellow or reddish yellow opaque eggs; blood capillaries showing.	Testes grow gradually in size; pinkish or flesh coloured; blood capillaries showing.
Stage III	Ripening 2 (R2)	Ovaries occupy about half of ventral cavity; reddish and numerous blood vessels; opaque eggs are now visible to naked eye and give the ovaries a granular appearance.	Testes occupy about half ventral cavity; begin to turn white, with fine, rather conspicuous blood vessels; no milt runs when pressure is applied.
Stage IV	Ripe (Ripe)	Has a few clear eggs at the earliest stage progressing to having mainly clear eggs but eggs do not extrude freely with slight pressure. Spawning has not started.	Testes distinctly wavy white and quite distended; large lobes; a small amount of milt may be forced out by pressure.
Stage V	Spawning (Sp'g)	As Stage IV but eggs running freely on slight pressure.	Testes very white and fully extended; milt runs freely at the slightest pressure.
Stage VI	Spent (Spent)	Ovaries soft; flabby and bloody; practically no eggs remain; purple in colour.	Testes shrunken and reddish; vas deferens prominent against irregular surfaces of testes; some blood left in organ.
Stage VII	Recovering (Rec)	Membrane purplish and ovaries fairly baggy, no eggs visible.	Testes resume pale pink colour; traces of blood in organ; vas deferens wrinkled and string-like.
Stage VIII	Resting (Rest)	Looks very much like Stage I, but is found in large fish; ovary larger than in Stage I, also membrane thicker and not as transparent as in Stage I.	Testes larger than in Stage I; surface regular, some greyish pink in colour.

descriptions of the various stages and augmented these with photographs. P. Koeller adopted these in the standard Marine Fish Division groundfish survey manual (unpubl. data). They have since been applied to cod (S. Gavaris, unpubl. data). As indicated by Halliday (1987), care must be taken when interpreting these data. For example, there is a fair degree of variability among samplers in the assigning of maturity stages. With the possible exception of the ripe or spawning stages, the demarcation between adjacent maturity stages is somewhat subjective. As Templeman et al. (1978) have indicated the problem is greater for males, particularly in assigning the spent condition. Because the first clear eggs develop in the lumen of the ovary, the demarcation between R2 and ripe in females may also be difficult unless the ovaries are cut open. In addition, for fish of both sexes near the average length at maturity, it is difficult to differentiate immature from resting stages. Hence, no attempt was made to discriminate between these stages except during spring when it was assumed that any fish not showing some sign of sexual maturation was immature. Because the length at first maturity is highly variable in other stocks (e.g. 37–73 cm for Barents Sea haddock (Blacker 1971 in Bergstad et al. 1987), it is not unreasonable to assume that, during the spawning season, even large "resting" haddock are actually immature. Unlike Templeman et al. (1978) we did not attempt to identify ripening virgins. The degree of overlap in the assigning of the adjacent maturity stages was evaluated by considering the magnitude and degree of variability in gonad weight for a given sex and stage.

Maturity stages were assigned to fish selected from stratified samples which were nonrandomized subsets of the total catch. To adjust for any bias caused by the stratified sampling, the total number of haddock of a given maturity stage (N_j) in a given set was calculated as:

$$N = \sum_i np_{ij}\, p_i \quad \text{where}$$

$$n = \sum_i n_i \,;\, p_{ij} = \frac{m_{ij}}{\sum_j m_{ij}} \text{ and } p_i = \frac{n_i}{\sum_i n_i} .$$

The quantity n is the total number of fish caught in a set in all i length categories (sum of n_i), p_{ij} is the proportion of m_{ij} (fish of i length category and j maturity) in the stratified sample and p_i is the proportion of fish of i length category in the catch. The numbers were adjusted to represent a standard 1.8-nautical mile two using a Western IIA trawl. Where a Yankee 36 trawl was used, a conversion factor of 1.2 was applied to the data (Fanning 1985). Plots of the number of haddock at each maturity stage were generated using the FORTRAN program MFD plot.dat1 (St. Andrews Biological Station, Marine Fish Division, St. Andrews, N.B.).

The length at which 50% of the population was mature was determined using Probit analysis, after Finney (1971, Statistical Package for the Social Sciences (SPSSX) version 3.1). Sample size varied from 491–8783 fish. This analysis which used only spring cruises (Table 1), assumed that mature fish would be at some stage of spawning condition (i.e. R1, R2, ripe, spawning, spent, or recovering) within 4–8 wk before peak spawning. Interannual and geographic differences in length at maturity were determined using relative median potency analyses (SPSSX, version 3.1). The geographic analysis was based on data from 1982–84 using the following areas (see Fig. 1): Browns Bank (stratum 80), Baccaro Bank (stratum 75), LaHave Bank (stratum 73), and approaches to the Bay of Fundy (strata 85 and 90). For interannual comparisons of length at maturity, data were combined for the following periods: 1970–72, 1974–76, 1977–79, 1980–82, and 1983–85. The composite lengths

TABLE 3. Least squares regression of gonad weight on body weight for Southwest Scotian Shelf haddock. Data were Log-transformed (both 10). All relationships were significant at $p<0.001$. The predicted gonad weight for a 1000 g fish is also indicated. The source of data used in the analysis is indicated in Table 1.

Stage	Intercept (SE)	Slope (SE)	*n*	r^2	Gonad wt. (g)
		Male			
Immature	−3.5511 (0.6036)	1.1283 (0.02604)	1094	0.632	0.68
Resting	−4.9772 (0.2007)	1.7241 (0.06540)	830	0.456	1.57
R1	−4.3484 (0.1556)	1.7830 (0.05249)	692	0.626	10.01
R2	−2.7446 (0.2390)	1.3119 (0.07921)	173	0.616	15.52
Ripe	−2.8693 (0.5558)	1.3015 (0.18141)	47	0.534	10.84
Spawning	−3.1309 (0.2365)	1.3543 (0.07600)	230	0.582	8.55
Spent	−3.9412 (0.1788)	1.4871 (0.05873)	503	0.561	3.31
Recovering	−4.7967 (0.1828)	1.7102 (0.06055)	505	0.613	2.16
		Female			
Immature	−3.5037 (0.0312)	1.4300 (0.01300)	1391	0.888	6.11
Resting	−3.4619 (0.0545)	1.4232 (0.01759)	1012	0.866	6.42
R1	−3.0379 (0.1242)	1.3044 (0.04174)	457	0.682	7.50
R2	−2.4974 (0.1575)	1.3255 (0.04926)	443	0.621	30.13
Ripe	−2.6125 (0.2245)	1.4624 (0.07093)	171	0.715	59.52
Spawning	−2.9644 (0.5690)	1.5741 (0.17509)	48	0.637	57.26
Spent	−3.8447 (0.3147)	1.5981 (0.10000)	127	0.671	8.90
Recovering	−3.2214 (0.1048)	1.3627 (0.03314)	430	0.798	7.36

at maturity for these periods were regressed against mid-year population biomass estimates (taken from O'Boyle and Wallace 1987).

Fecundity and gonad weight analyses were based on data collected on six standard or dedicated groundfish cruises (1983–86) (Table 1). The fish were measured to the nearest centimetre (fork length), placed in labelled polyethylene bags and frozen. In the laboratory, the haddock were weighed to the nearest 0.1 g and the otoliths and ovaries were removed. Only ovaries in the R2 stage of maturity (ripe but with no hydrated eggs) were chosen for fecundity determination. These were weighed to the nearest 0.01 g, placed in modified Gilson's fluid (Simpson 1951) and after at least 3 wk, shaken vigorously using a 186 W Eberbach platform shaker (model 6000). When the eggs were freed from the ovarian membranes, they were rinsed in water and placed in 5% formalin (by volume). The ovary samples were then sieved consecutively through 1000- and 250-μm mesh screens constructed of monofilament polyester (B&SH Thompson and Co. Ltd, Montreal PQ), which was chosen for its resistance to Gilson's fluid. The larger mesh retained the ovarian connective tissue and blood vessels while the smaller retained all eggs which would have been spawned that year (Raitt 1933; Hodder 1963; Alekseyeva and Tormosova 1980). The freed eggs were placed in a whirling vessel (Wiborg 1951) which fractioned the sample into tenths. This procedure was repeated twice so that the sample counted represented 1/1000 of the total freed eggs. The procedure used was similar to that described in Hodder (1963) except that we counted four rather than two subsamples from the 1/1000 splitting thereby duplicating Hodder's procedure from the initial 1/10 splitting. A minimum of about 300 eggs was counted in each subsample using a dissecting microscope. Hence if the ovary was too small, four samples from the 1/100 splitting were used. If the coefficient of variation (CV) for the four subsamples was greater than 10%, the splitting and counting procedures were repeated and the original data were not used. Because only one ovary was processed, total fecundity was calculated from the total weight of the two ovaries assuming the relative fecundity of the ovaries (eggs/gram) was not significantly different. In the absence of histological data on the extent of resorbed eggs, we could not adjust fecundity estimates as suggested by Robb (1982). Hence our values may be overestimated by about 6%.

The relationship between fecundity and length or weight is usually expressed in the form: fecundity = $a \times \text{length}^b$ (or fecundity = $a \times \text{weight}^b$, Bagenal 1978). To linearize these relationships and to induce homogeneity of variance over the range of observations, we Log-transformed (base 10) and fitted the data using least squares regression (e.g. Log fecundity = $a + b$ Log length). Using analysis of covariance (STSC Statgraphics, version 2.6), we compared the following areas within NAFO Division 4X (see Fig. 1): Browns Bank (stratum 80), the area surrounding Browns Bank (stratum 81), areas to the east of Browns Bank (strata 70, 72–77), and the Bay of Fundy area (strata 85, 90–95).

Relationships between body and gonad weight were determined, by sex, for the various maturity stages. To induce homogeneity of variance over the range of observations, we again Log-transformed and fitted the data using least squares regression. Inspection of the residuals indicated that this transformation was appropriate. Statistical differences between groups were determined using analysis of covariance with body weight as covariate.

Results

Gonad Weight in Relation to Maturity Stage and Sex

With the exception of the R1 stage, ovaries were always larger ($p<0.001$) than testes at a given maturity stage (Table 3). This was most evident in the R2, ripe, and spawning stages where ovaries were 4–6 times heavier than testes. However, the relative difference in gonad weight (maximum/minimum) was similar for both sexes. The relationships between body weight and gonad weight were more variable in males than in females

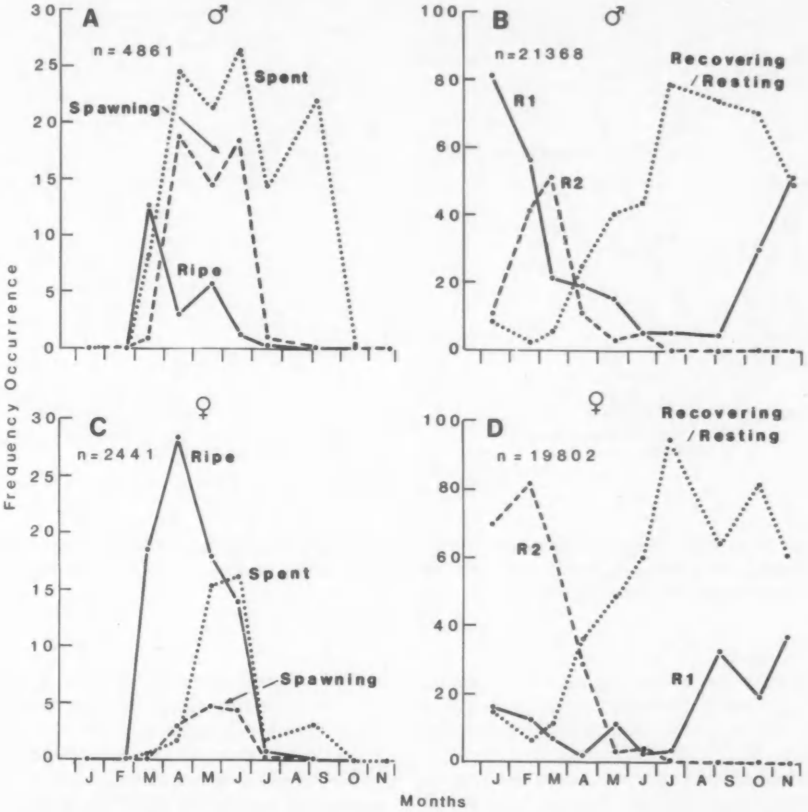


FIG. 2. Frequency of occurrence, expressed as percentage of maturity stages for Southwest Scotian Shelf haddock at different times of the year over the period 1970–75 (see Table 1). Only fish larger than the length at maturity were included in the analysis. Panel A and B = male; panel C and D = female haddock. Data were adjusted for catch composition.

(Table 3). In females, the gonads increased in weight from the resting through to the ripe condition but did not significantly decrease during spawning despite the release of eggs. In contrast, testes increased in weight to the R2 stage and declined thereafter. The significant decline between R2 and ripe stages suggests that the criteria used to differentiate ripe versus spawning condition were inappropriate and that "ripe" males had already started spawning. Analysis of covariance indicated significant differences in gonad weight between adjacent maturity stages with the exception of resting versus immature for females and ripe versus spawning for males and females, however, many of these differences were small, and there was considerable overlap in gonad size between adjacent stages.

Seasonal Maturation Cycle

The annual reproductive cycle was tracked by plotting the percent frequency of occurrence of the various maturity stages at different times of the year (Fig. 2). The proportion of haddock in the resting/recovering categories increased over the early summer peaking in late July. In the late summer and early autumn, the occurrence of R1 fish increased, peaking between November and January for males and September to November for females (Fig. 2B and D). Fish in R2 condition were most prevalent in February and March while ripe fish were most abundant in March to May or June. Spawning fish were found between March and August but the peak in percent occurrence was April to June (Fig. 2A and C). However, there were differences in this general pattern between males and females. The peak period for the spawning condition was longer and occurred earlier in males. The proportion of ripe fish was lower in males than in females while the opposite was noted for the spawning condition.

The gonad weight of maturing males reached a maximum in February and March (Fig. 3) when it accounted for 1–2.2% of the total body weight. It declined steadily during and following spawning reaching a minimum of about 0.05–0.5% body weight in August to October. Thereafter, testis weight slowly increased during the winter. Ovary weight peaked later than testis weight (end of March to the middle of May). Ripe ovaries were 3.1–12.5% of body weight. After spawning, the ovary weights declined to their lowest levels (end of July to October). Resting ovaries accounted for 0.32–1.27% of body weight.

Distribution by Maturity Stage

In the early spring, the greatest concentrations of haddock were found in the area of the offshore banks, mainly Browns

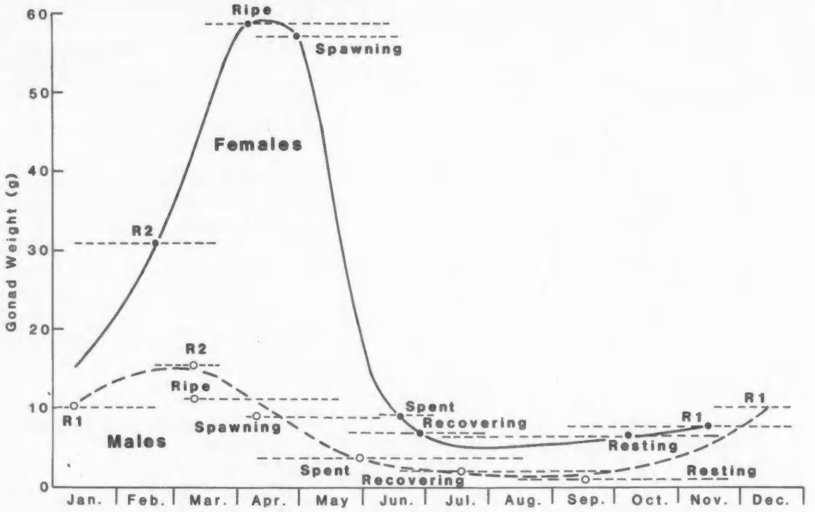


FIG. 3. Seasonal changes in the weight of ovaries and testes calculated for 1000 g fish. Points are located at the period of highest occurrence of the respective stages. Dashed lines indicate the duration of peak occurrence of the stage (see Fig. 2).

and Baccaro. This pattern was evident for both sexes and all maturity stages (Figs. 4 and 5). However, significant catches of immature and R1 fish were also taken in the approaches to the Bay of Fundy (Figs. 4A,B and 5A). The distribution of R2, ripe, and spawning haddock was more contracted and more or less restricted to Browns Bank, the area between Browns and Baccaro Banks and LaHave Bank. The pattern for spent fish was similar but less concentrated than for spawning fish.

In the summer, the limited number of ripe and spawning fish was also restricted to the offshore banks but to a much greater extent on LaHave and Roseway Banks (Figs. 6 and 7). Apart from a few spawning males and females found off Cape St. Mary (Figs. 1, 6, and 7), there was virtually no evidence (spring or summer) for spawning activity in the mouth of the Bay of Fundy or in the Bay of Fundy proper. The relatively widespread distribution of spent and recovering male and female haddock in the summer suggests that fish leave the spawning grounds soon after they have spawned.

Superimposing the distribution of ripe and spawning haddock on a corresponding map of the surficial geology (from Fader et al. 1977; Drapeau and King 1972) revealed that the majority of spawning, spent, and ripe fish were found over Sable Island gravel and sand. Over 95% of all spawning fish were found over sand/gravel mixtures. The most highly selected mixture was composed of "...clean, buff to greyish brown, medium- to coarse-grained, very well sorted sand grading laterally to very coarse gravel..." with sand contributing less than 50% (Drapeau and King 1972). Ripe haddock tended to be less selective with respect to substrate than were spawning fish (Fig. 8).

The preferred depth for all maturity stages was 40–60 fms (Fig. 9). However, the percent occurrence outside this depth range varied with maturity stage (e.g. 58% for recovering or R1, 43% for immature and 63% for large immature/resting fish). For haddock in ripe, spawning, or R2 condition, the percent occurrence outside the 40–60 fm depth range was only 31 to 38%.

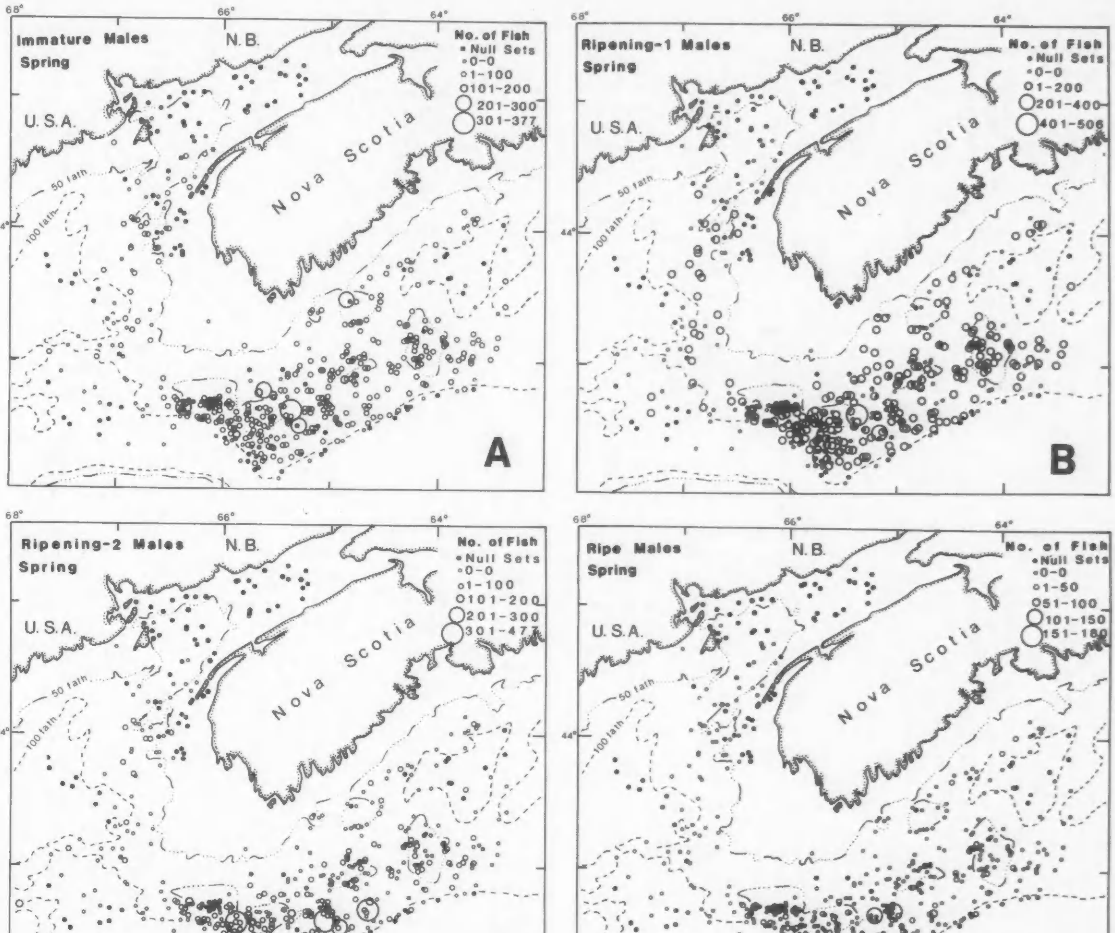
Preferred modal spring temperatures varied over the range 3–9°C (Fig. 10). Fish in immature, R1, R2, spent, and recovering stages were well represented within this temperature range. However, there was a distinct shift in temperature preference, to colder water, in ripe and spawning haddock. The range of temperatures occupied by fish in these maturity stages was also contracted (Fig. 10). Over 76% of spawning fish were found at water temperatures of 1–5°C.

The pattern with salinity was similar to that of temperature but was less dramatic. With the exception of fish in the spawning or spent category, haddock inhabited water within the 32–35 ppt salinity range (Fig. 11). Spawning and spent fish were more restricted to 32–34 ppt salinity.

Length at Maturity

The length at first maturity for all years, based on spring survey data, was 36.36 and 42.58 cm, respectively for males and females (Fig. 12). Lengths at 50% maturity for females were higher ($p<0.05$) than corresponding values for males which exhibited a higher variability in estimates (Fig. 13). The smallest mature male and female weighed 125 and 200 g, respectively. There were also significant differences in length

FIG. 4. Spring distribution of male haddock at different stages of sexual maturation. A = immature, B = R1, C = R2, D = Ripe, E = spawning, F = spent. Zero values (small open circles) indicate that no haddock were caught of the corresponding maturity stage; null sets (small closed circles) are sets with no haddock caught. Cruise coverage is given in Table 1. Numbers represent total numbers caught per standard tow, adjusted for catch composition.


Immature Males Spring

Ripening-1 Males Spring

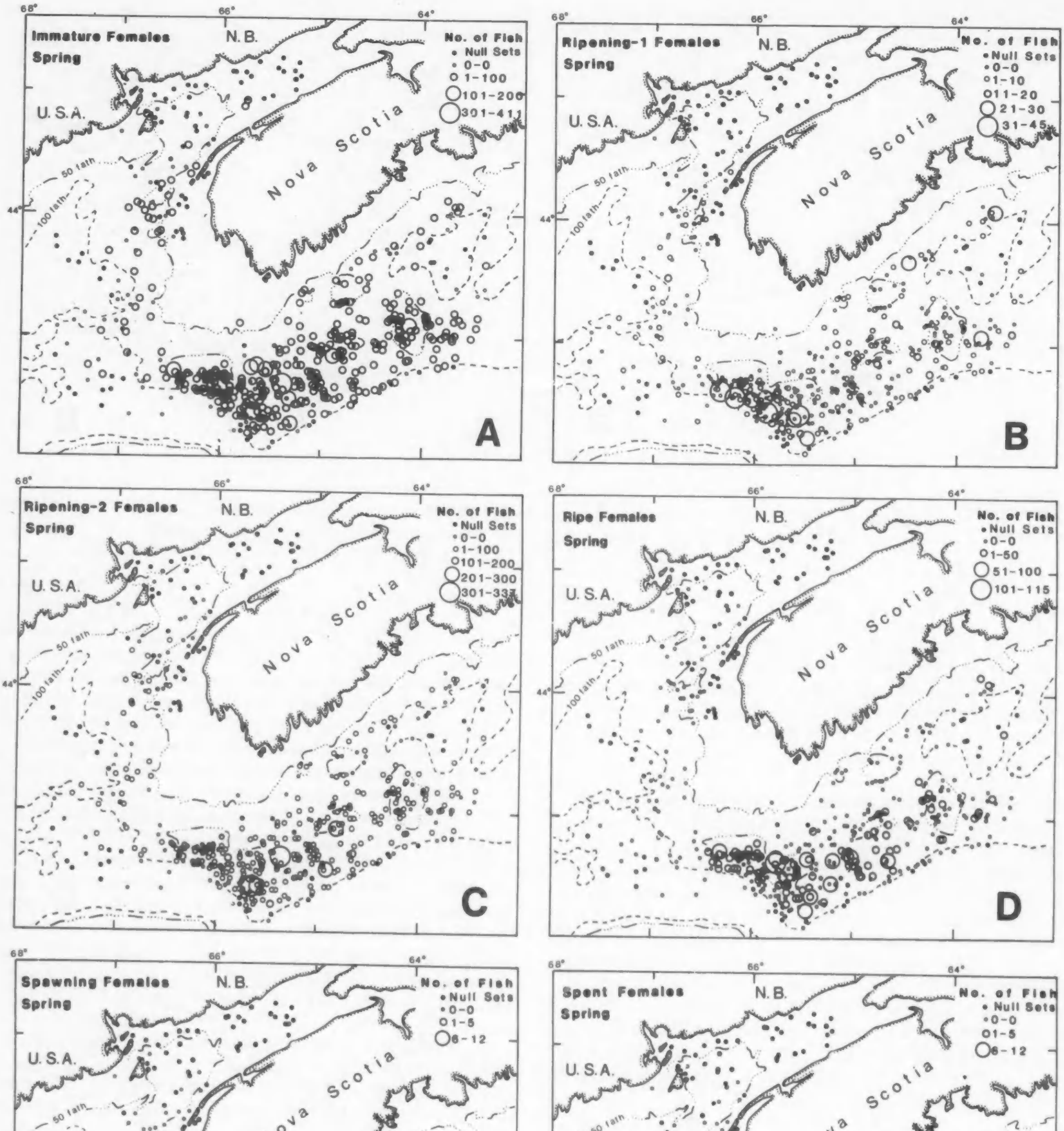
Ripening-2 Males Spring

Ripe Males Spring

Spawning Males Spring

Spent Males Spring

68°
66°
64°
44°
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
No. of Fish
• Null Sets
∘ 0-0
○ 1-100
○ 101-200
○ 201-300
○ 301-377
A
No. of Fish
• Null Sets
∘ 0-0
○ 1-200
○ 201-400
○ 401-506
B
No. of Fish
• Null Sets
∘ 0-0
○ 1-100
○ 101-200
○ 201-300
○ 301-477
C
No. of Fish
• Null Sets
∘ 0-0
○ 1-50
○ 51-100
○ 101-150
○ 151-180
D
No. of Fish
• Null Sets
∘ 0-0
○ 1-10
○ 11-20
○ 31-39
E
No. of Fish
• Null Sets
∘ 0-0
○ 1-20
○ 21-40
○ 41-60
○ 61-88
F


68°
66°
64°
44°
Immature Females
Spring
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
No. of Fish
Null Sets
0-0
1-100
101-200
301-411
A
Ripening-1 Females
Spring
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
No. of Fish
Null Sets
0-0
1-10
11-20
21-30
31-45
B
Ripening-2 Females
Spring
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
No. of Fish
Null Sets
0-0
1-100
101-200
201-300
301-337
C
Ripe Females
Spring
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
No. of Fish
Null Sets
0-0
1-50
51-100
101-115
D
Spawning Females
Spring
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
No. of Fish
Null Sets
0-0
1-5
6-12
E
Spent Females
Spring
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
No. of Fish
Null Sets
0-0
1-5
6-12
F

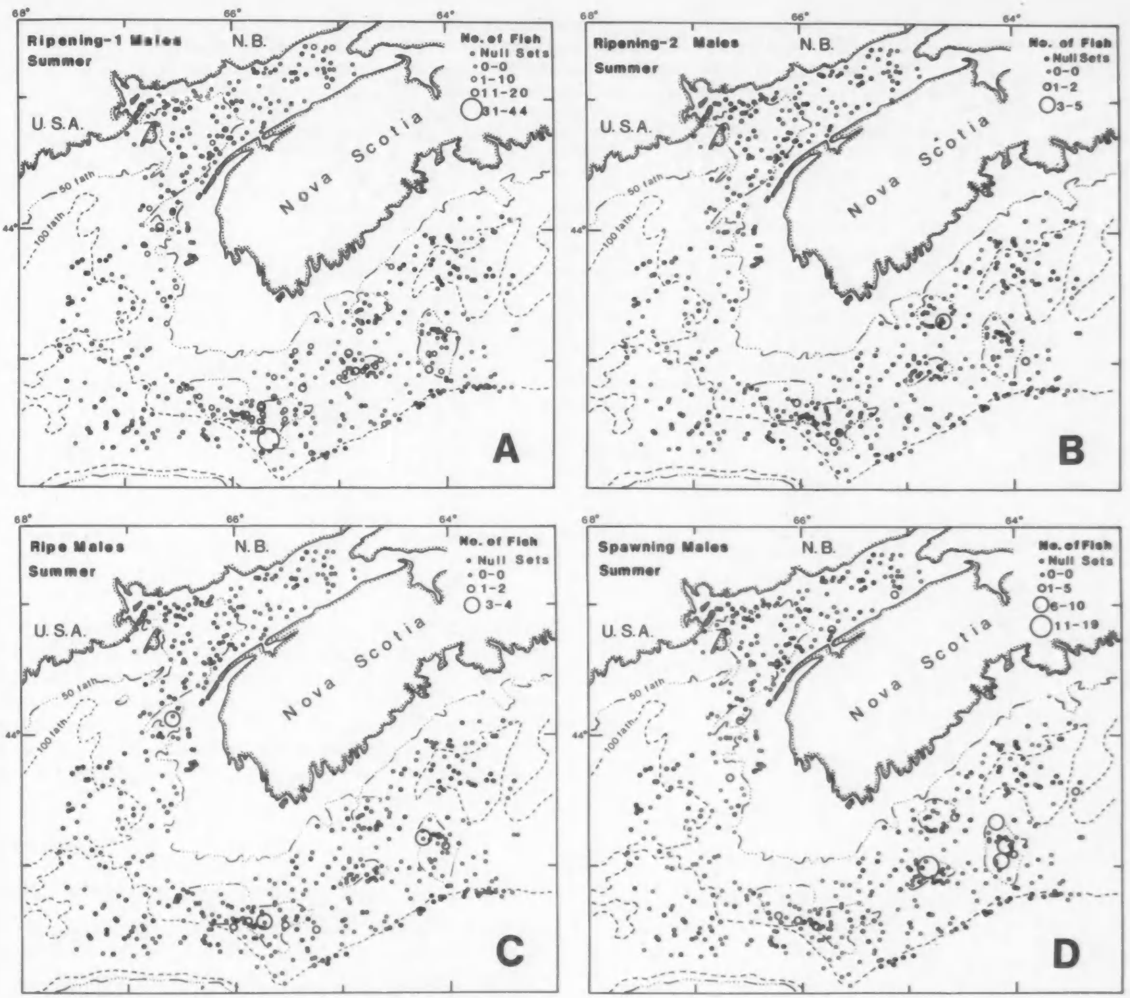

68°
66°
64°
44°
Ripening-1 Males
Summer
Ripening-2 Males
Summer
Ripe Males
Summer
Spawning Males
Summer
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
No. of Fish
• Null Sets
• 0-0
○ 1-10
○ 11-20
○ 31-44
No. of Fish
• Null Sets
• 0-0
○ 1-2
○ 3-5
No. of Fish
• Null Sets
• 0-0
○ 1-2
○ 3-4
No. of Fish
• Null Sets
• 0-0
○ 1-5
○ 6-10
○ 11-19
A
B
C
D

FIG. 6. Summer distribution of male haddock at different stages of sexual maturation. A = R1, B = R2, C = ripe, and D = spawning. Zero and null set values are defined in Fig. 4. Cruise coverage is given in Table 1. Numbers represent total numbers caught per standard tow, adjusted for catch composition.

at first maturity over the 15-yr period (Fig. 13). The lowest levels for males and females were observed during 1970–72. Thereafter they increased to the highest values in 1980–82 and decreased again during 1983–85. Relative median potency analysis indicated that lengths at 50% maturity for 1970–72 were lower ($p<0.05$) than corresponding values for all other periods with the exception of 1974–76. For males, 1980–82 was significantly higher than all other periods while for females, 1980–82 was significantly higher than 1970–72, 1974–76 and 1983–85. There was a positive ($p<0.01$) relationship (Fig. 14) between the length at 50% maturity and the mid-year biomass (from O'Boyle and Wallace 1987). The correlation coefficient was higher in females than in males.

Fecundity

Analysis of covariance indicated no significant difference in the fecundity/length or fecundity/weight relationship due to year (Table 4). Similarly, there was no significant difference in these relationships among four areas within 4X including: Browns Bank proper, area surrounding Browns Bank, Bay of Fundy and approaches, and the area to the northeast of Browns Bank

FIG. 5. Spring distribution of female haddock at different stages of sexual maturation. A = immature, B = R1, C = R2, D = Ripe, E = spawning, and F = spent. Zero and null set values are defined in Fig. 4. Cruise coverage is given in Table 1. Numbers represent total numbers caught per standard tow, adjusted for catch composition.

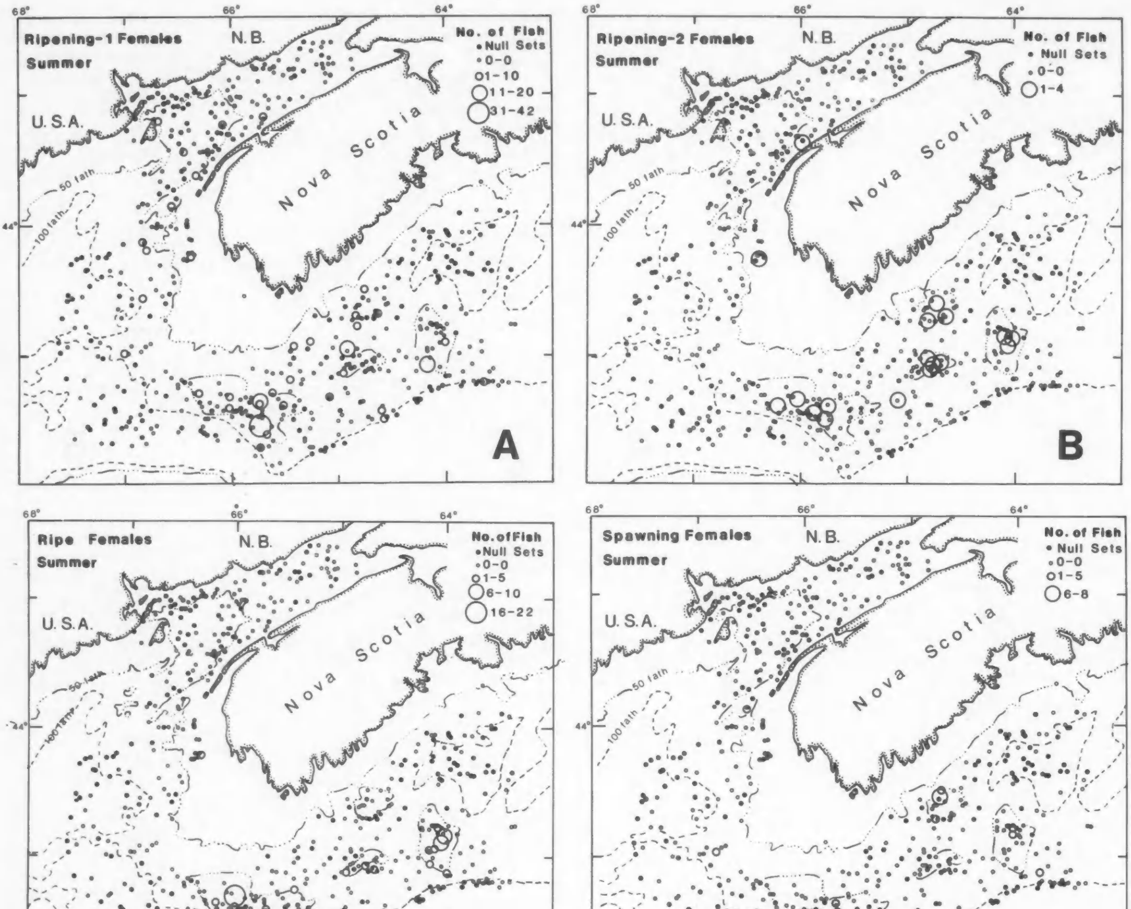

68°
66°
64°
44°
Ripening-1 Females
Summer
No. of Fish
• Null Sets
◦ 0-0
○ 1-10
○ 11-20
○ 31-42
N.B.
U.S.A.
Nova Scotia
50 fath
100 fath
A
Ripening-2 Females
Summer
No. of Fish
• Null Sets
◦ 0-0
○ 1-4
B
Ripe Females
Summer
No. of Fish
• Null Sets
◦ 0-0
○ 1-5
○ 6-10
○ 16-22
C
Spawning Females
Summer
No. of Fish
• Null Sets
◦ 0-0
○ 1-5
○ 6-8
D
Spent Females
Summer
No. of Fish
• Null Sets
◦ 0-0
○ 1-5
○ 6-10
○ 11-14
E

FIG. 7. Summer distribution of female haddock at different stages of sexual maturation. A = R1, B = R2, C = Ripe, D = spawning, and E = spent. Zero and null set values are defined in Fig. 4. Cruise coverage is given in Table 1. Numbers represent total numbers caught per standard tow, adjusted for catch composition.

TABLE 4. Fecundity/length fecundity/weight and fecundity/age relationships for Southwest Scotian Shelf haddock. Relationships are expressed as: Log Fecundity = $a + b$ Log Length (or weight) where length is in centimetres and weight is in grams. Age was not transformed. BB = Browns Bank; SBB = area surrounding Browns Bank; ABF = Bay of Fundy and approaches; NEBB = northeast of Browns Bank; P1 = day 5–20; P2 = day 55–67; P3 = day 68–74; P4 = day 75–85; P5 = day 86–100.

Subset	Independent variable	Slope (b)	Intercept (a)	r^2	SE of estimate	n
all	Log length	3.1225	0.34560	7372	0.12535	405
all	Log weight	1.0452	2.38989	7756	0.11387	378
1983	Log length	3.1975	0.21826	7152	0.84567	145
1984	Log length	3.3994	−0.31315	7555	0.13570	48
1985	Log length	3.1290	0.33911	7546	0.12924	114
1986	Log length	2.9314	0.68366	7266	0.85239	98
BB	Log length	2.9900	0.58061	6836	0.14138	96
SBB	Log length	3.3891	−0.10056	7774	0.12613	74
ABF	Log length	3.8449	−0.93448	6332	0.13208	30
NEBB	Log length	3.0619	0.44334	7642	0.11571	202
P1	Log length	3.2725	0.08452	6989	0.12478	122
P2	Log length	2.9637	0.62858	7019	0.12281	87
P3	Log length	3.0780	0.42909	7573	0.11517	125
P4	Log length	3.4662	−0.25877	7827	0.13277	52
P5	Log length	2.3958	1.52133	5903	0.16361	19
all	age	0.1462	5.02592	4343	0.19380	160

(Table 4). Multiple regression including a quadratic term for time of year indicated that fecundity for a given length declined ($p<0.02$) over the period January to April (Fig. 15). However the decline was relatively small (about 15%) and the quadratic terms explained less than 1% of the observed variability in fecundity. The relationship between fecundity and age had a lower correlation coefficient than for either length or weight (Table 4).

Discussion

Gonad Weight in Relation to Maturity Stage and Sex

The pattern of gonad weight increase with maturation was consistent with that described earlier (Templeman et al. 1978 and Templeman and Bishop 1979). The relationships between gonad weight and body weight had slopes greater than 1 indicating that caution should be taken when comparing maturity stages on the basis of gonadosomatic indices (100 × gonad wt/body wt). For example, the predicted ovary weight of a 500-g haddock was 21.6 g or 4.32% of body weight. The corresponding values for a 6300-g haddock were 878.3 g and 13.94% a four-fold difference in gonadosomatic index. This agrees with the findings of DeVlaming et al. (1982) and Roff (1983). The higher variability in gonad/body weight relationships shown by males is unexplained. A possible contributor to this is the degree to which mesenteries are included in the weight when the testes are removed. However this effect would be minimal in the more advanced stages of sexual maturation where the high variability was still observed. It is also interesting to note the large difference in size between ripe ovaries and testes. If gonad size is related to energy expenditure then, on the basis of this alone, one would expect

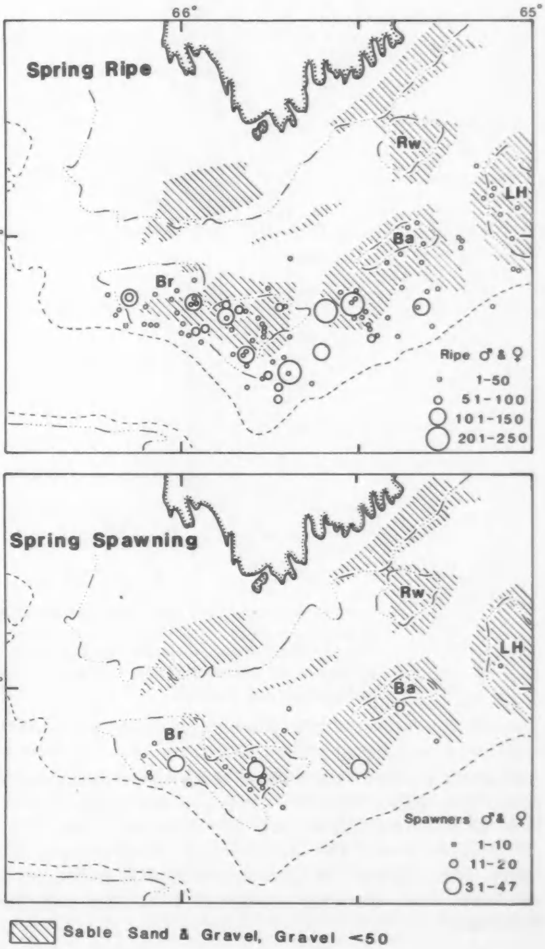


FIG. 8. Distribution of ripe and spawning 4X haddock in relation to substrate type (see Gordon et al. 1972 and Drapeau and King 1972 for detailed description of substrate types). Cruise coverage is given in Table 1.

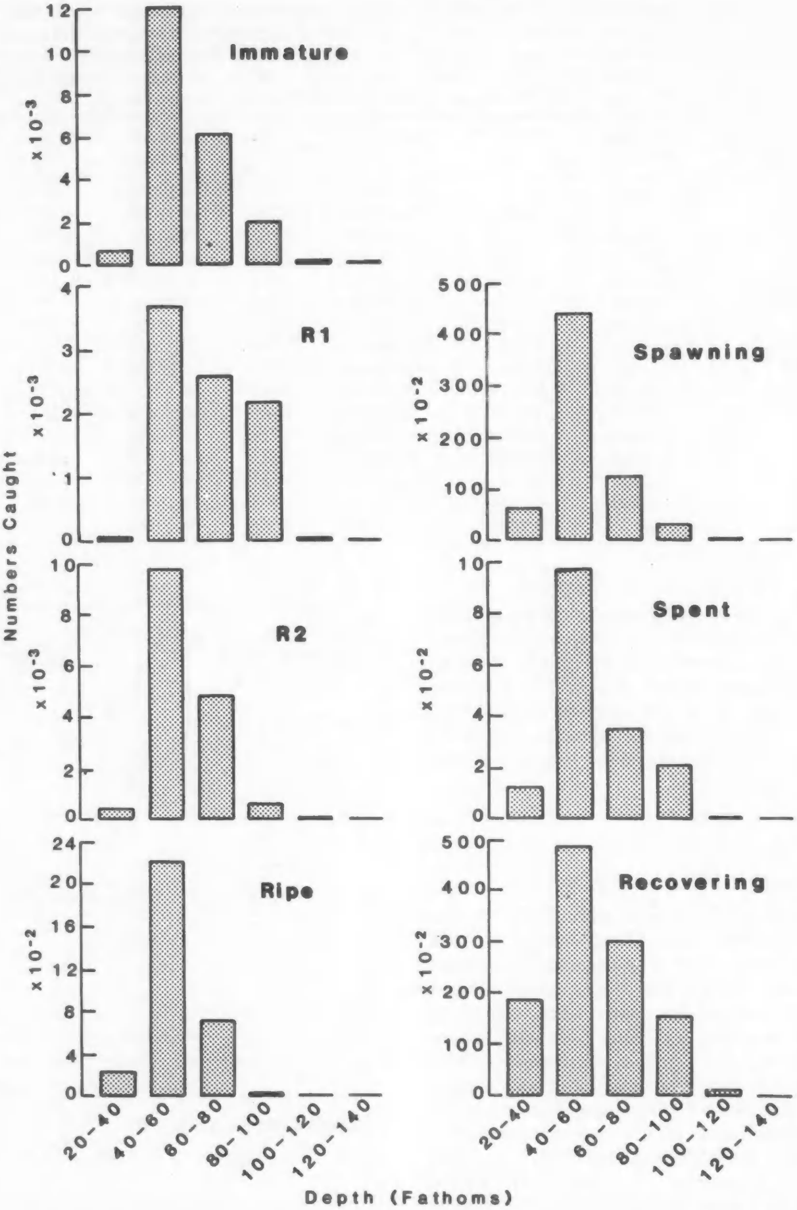


FIG. 9. Occurrence of different maturity stages (males and females combined) in relation to depth. Only spring cruises were used (Table 1). Values are total numbers adjusted for catch composition (see equation in Materials and Methods).

differences in growth rates between sexes with females growing slower than males. However, not only is this not the case for haddock but where differences in growth between sexes occurs (for example, in most flatfish species), it is the females that are larger. This suggests that other factors such as differences in maturation rate, spawning activity, or food intake are also important.

One other important difference between males and females was the pattern of gonad weight loss during spawning. Ovaries tended to retain their weight during spawning whereas testes continually lost weight. This suggests that the loss of spawned eggs is made up by the hydration of new eggs — a process that will continue throughout the spawning period. In males, spent sperm is either not replaced or replaced at a rate much slower

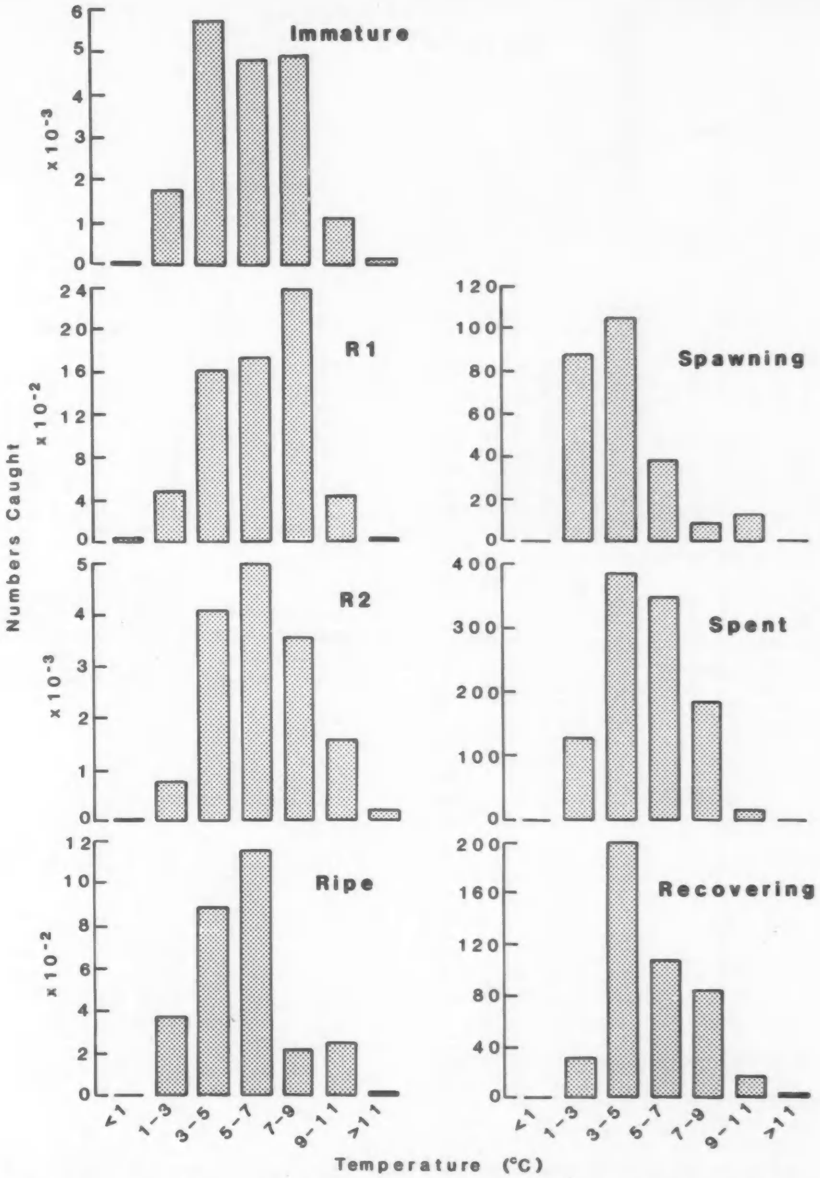


FIG. 10. Occurrence of different maturity stages (males and females combined) in relation to temperature. Only spring cruises were used (Table 1). Values are total numbers adjusted for catch composition (see equation in Materials and Methods).

than the rate of loss. In fact, the lower weight of ripe compared with R2 testes suggests that the 'ripe' category may be incorrectly assigned to an early spawning condition.

Seasonal Maturation Cycle

The low occurrence of spawning fish, particularly females, may be due to several reasons including: the area of spawning was not sampled adequately, spawning fish were less available to the bottom gear (e.g. spawning occurs in midwater), haddock release eggs in the process of capture (as suggested by Htun-Han (1978) for dab *Limanda limanda*), or simply that the time when the fish are in the process of spawning is very short thereby reducing the probability of being captured in that condition. Given our current knowledge of the fishery and the survey coverage, it is unlikely that major spawning areas would remain unknown. One exception may be the unsurveyed area to the northwest of Browns Bank. There is some evidence that

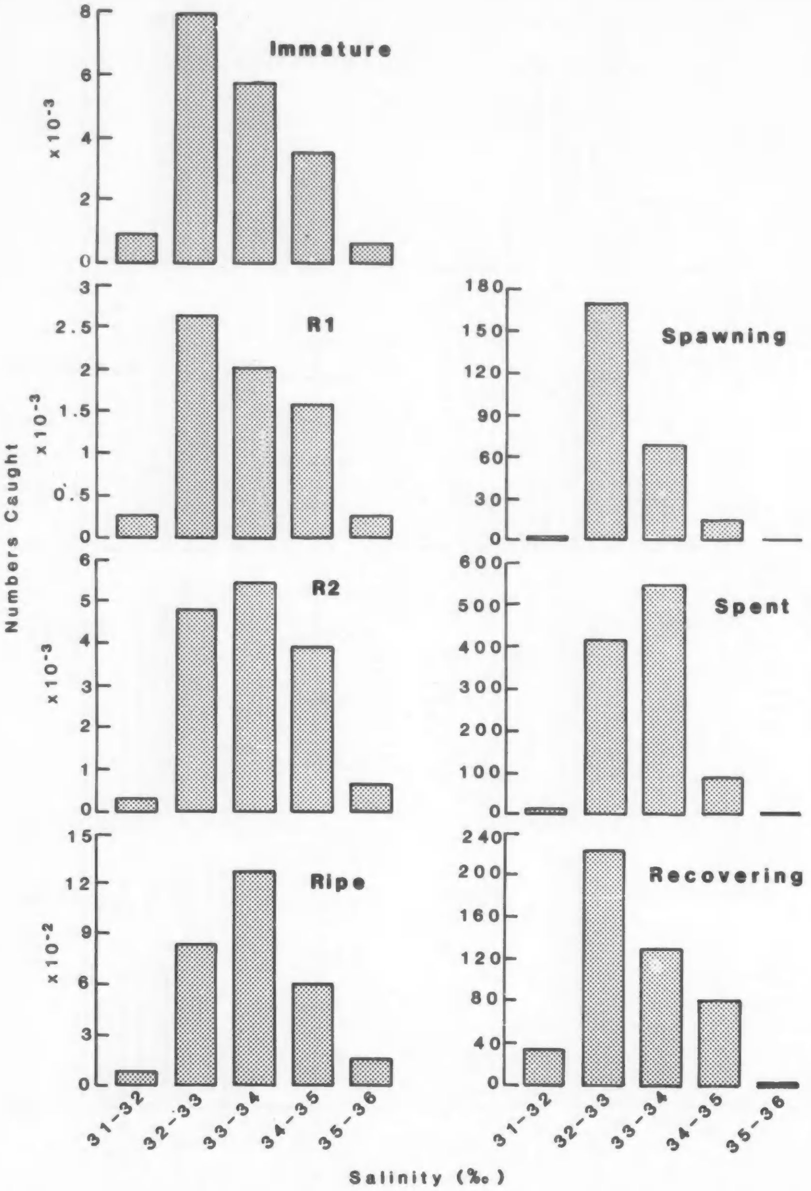


FIG. 11. Occurrence of different maturity stages (males and females combined) in relation to salinity. Only spring cruises were used (Table 1). Values are total numbers adjusted for catch composition (see equation in Materials and Methods).

spawning is benthic or at least bathypelagic (Trout 1962, in Hawkins et al. 1967) and hence spawning fish should be available to the survey trawls. On the other hand there is good evidence that female haddock spawn only at intervals of 1 to 2 d for 2–3 wk (Hawkins et al. 1967). Hence the probability of catching spawning females would be low. The relatively low percent occurrence of males in the ripe category suggests that either this category is inappropriate or that these fish quickly pass through this stage.

From the analysis of the proportion of maturity stages at different times of the year we may conclude that major spawning occurs from mid-April to mid-June. This is later in the spring than noted by Scott (1983). Based on ichthyoplankton surveys, O'Boyle et al. (1984) demonstrated that haddock eggs peaked

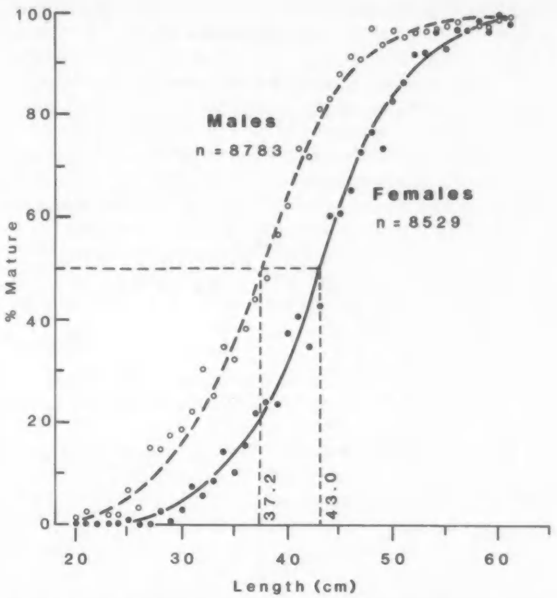


FIG. 12. Maturity ogives for Southwest Scotian Shelf haddock. Data are combined from spring surveys 1970–72 and 1974–85. Values were adjusted to account for catch composition (see equation in Materials and Methods). Numbers in figure indicate sample size.

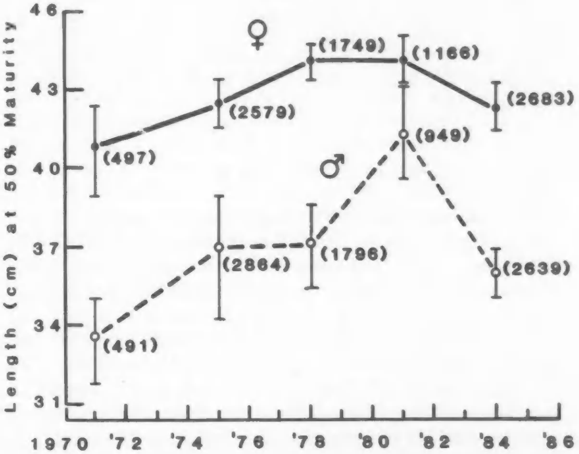


FIG. 13. Lengths at 50% maturity for male and female haddock from the Southwest Scotian Shelf. Data are combined from spring cruises for years 1970–72, 1974–76, 1977–79, 1980–82, and 1983–85. Sample sizes are indicated in parentheses. Bars represent 95% CI.

in abundance in April and May, but Hurley and Campana (1989) presented data to suggest that peak spawning may extend into June in some years. Our data are in agreement with these latter studies. It must be remembered, however, that these conclusions are based on combined data for several years, and it is likely that peak spawning from year to year can vary by over 3 mo (Colton 1968 and Marak and Livingstone 1970). Similarly

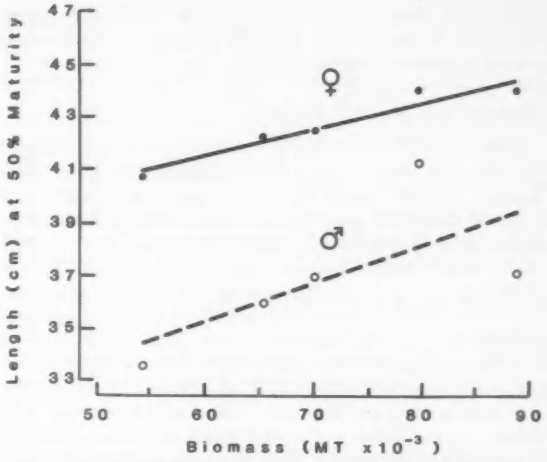


FIG. 14. Lengths at 50% maturity for male and female haddock from the Southwest Scotian Shelf as a function of mid-year stock biomass from O'Boyle and Wallace, (1987). Data are combined from spring cruises for years 1970–72, 1974–76, 1977–79, 1980–82, and 1983–85. Sample sizes are indicated in Table 5.

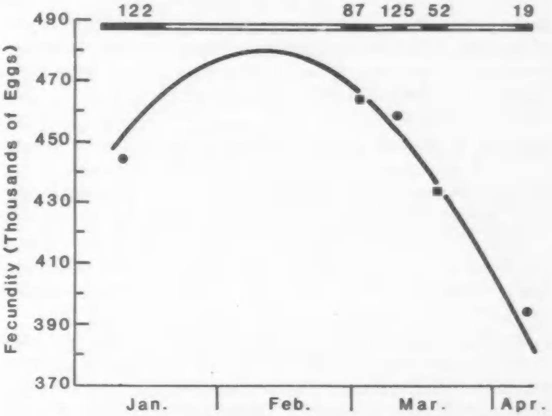


FIG. 15. Seasonal variation in the fecundity of a 50-cm haddock from the relationship: Log fecundity = 0.34455 + 3.11286 (Log length) + 0.002361 (day of year) − 0.000029 (day of year)^2; $n=405$, $r^2=0.74$, $p<0.02$. The points represent corresponding values from individual fecundity/length equations for the sampling periods indicated in the upper horizontal bar.

the duration of peak spawning may also vary from year to year (Marak and Livingstone 1970). With the exception of St. Pierre and Grand Banks haddock, which tend to spawn later (Templeman and Bishop 1979; Templeman et al. 1978), peak spawning periods do not vary greatly for stocks on both sides of the Atlantic (Colton 1965; Marak and Livingstone 1970; Overholtz 1987; Alekseyeva and Tormosova 1980).

Spawning area closures for haddock in the Browns Bank area have been enforced since 1970 and the current period of restriction is March–May (Halliday 1988). Although our data suggest that significant spawning may occur well into June, we note that, despite the relatively high proportion of spawning fish in

June, the absolute numbers of fish may be small due to migration out of the areas being sampled. Closure in March would protect prespawning rather than spawning fish.

Distribution by Maturity Stage

Distributions of haddock at different maturity stages indicate that spawning and prespawning fish aggregate on the offshore banks as noted by Scott (1983). This study further shows that as sexual maturation progresses the distribution is further contracted until spring spawning haddock occupy a relatively small portion of the Browns/Baccaro Bank area. In the summer, the remaining spawners are found mostly on Roseway, Baccaro, and LaHave Banks. Generally, our findings agree well with egg distributions from ichthyoplankton surveys in 4X. O'Boyle et al. (1984) and Hurley and Campana (1989) showed haddock egg concentrations over Browns Bank. The lack of evidence for eggs from LaHave and Roseway Banks could be explained by deficiencies in temporal or spatial coverage in these studies.

Circulation over Browns Bank is dominated by tidal effects which induce a permanent gyre around the bank (Smith 1983; 1989). The importance of circulation and other factors in relation to larval retention and survival on Browns Bank was discussed by O'Boyle et al. (1984) and several authors in this issue (Smith 1989; Frank et al. 1989; Campana et al. 1989; and Page et al. 1989). It is interesting to note that although haddock are widely distributed in the waters off Southwest Nova Scotia and in the Bay of Fundy, virtually no spawning occurs in the mouth of the Bay of Fundy or in the Bay of Fundy proper. However, some areas were not surveyed including: a large area to the northwest of Browns Bank with untrawlable bottom, inshore areas less than 50 fathoms and coastal shelf greater than 200 fathoms. In periods of high abundance, the spawning may be extended into less utilized areas. Notwithstanding this, our findings support the view that offshore haddock from the Southwest Scotian Shelf and southern Bay of Fundy are comprised of only one spawning unit (stock). This is also supported by haddock egg and larval distributions (see Hurley and Campana 1989; Frank et al. 1989). This does not exclude the possibility of local inshore populations.

It is interesting to note that spawning is virtually restricted to one type of substrate (Sable Island sand and gravel mixture) which, in NAFO division 4X is limited to a few areas including Browns, Baccaro, LaHave, and Roseway Banks three inshore areas off Yarmouth, Cape Sable and Lockeport, and a few isolated shoals. Of the inshore areas, spawning has also been reported on the Lockeport grounds (Kohler 1959). This substrate is even present in the area off Cape St. Mary where small numbers of spawning haddock were found (Figs. 1, 6, and 7). The importance of substrate in spawning behaviour is not known. However, the apparent absence of spawning in other areas of 4X may be related to the lack of suitable substrate.

Because they are interrelated and confounded, it is difficult to determine the relative importance of temperature, depth, or salinity as directive or cueing factors for spawning aggregation. What is clear is that spawning or near-spawning fish select more restricted temperatures and salinities. The pattern for depth is less clear. In the case of temperature, there seems to be a distinct shift in occupation to lower temperatures in spawning fish. Overholtz (1987) found that maturing Georges Bank haddock inhabited water of 4–7°C. Similar values (3.3–5.6°C) were reported by Marak and Livingstone (1970). With the exception of the spawning category, where the temperatures occupied are lower, our results are in agreement with these findings.

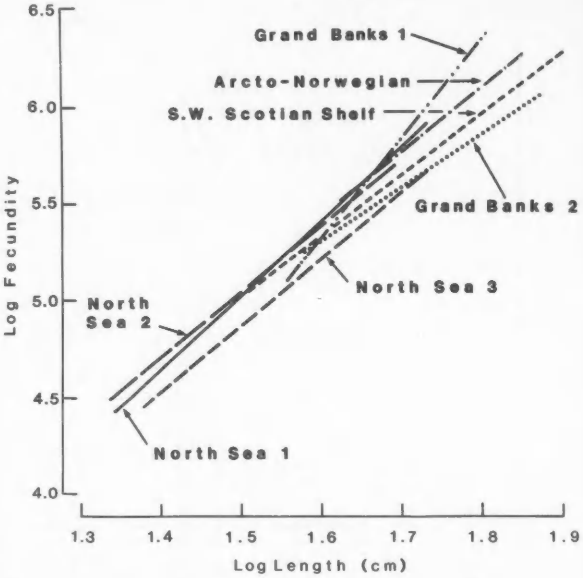


FIG. 16. Fecundity/length relationships for different haddock stocks. Original equations or data have been adjusted to conform to the equation Log fecundity = $b + a$ Log fork length (Log $F = a$ Log L). Fork length = total length × 0.975. Where unspecified, fork length was assumed. North Sea^1 — Log $F = -0.692 + 3.840$ Log L (from Raitt 1933). North Sea^2 — Log $F = -0.44 + 3.420$ Log L (from Hislop and Shanks 1979). North Sea^3 — Log $F = -0.312 + 3.45$ Log L (from Alekseyeva and Tromosova 1980). Arcto-Norwegian — Log $F = -.0999 + 3.343$ Log L (from Sonina 1971). Grand Banks^1 — Log $F = -2.857 + 5.11$ Log L (Hodder 1963). Grand Banks^2 — $0.847 + 2.792$ Log L (Rojo 1955). Southwest Scotian Shelf — Log $F = 0.3456 + 3.122$ Log L (this paper).

Length at Maturity

Southwest Scotian Shelf haddock are larger at maturation than haddock from the North Sea (Hislop and Shanks 1979) and Georges Bank (Overholtz 1987) but are slightly smaller at maturation than haddock from the St. Pierre and Grand Banks (Templeman and Bishop 1979; Templeman et al. 1978). Our results agree well with those of Kohler (1959), who evaluated an inshore population in the Lockeport area off Southwest Nova Scotia but are slightly lower for the same period than those given in Beacham (1983). This could be attributed to differences in the time of sampling (early spring versus July). The use of summer cruises for determining length at maturity was rejected in this study since differentiation between resting and immature condition in young fish is extremely difficult and immature stages are often ascribed on the basis of length (the very parameter being determined). These serious problems have been discussed at length by Halliday (1987). Beacham (1983) concluded that the median length at maturity remained relatively constant over the study period (1958–79) although his data indicate a relatively wide range, 32–52 cm for males and 35–47.5 cm for females. Our lengths at 50% maturity varied from 33.56–41.23 cm for males and 40.76–44.04 cm for females.

Interannual variation in the length and age at maturity has been found for several haddock stocks including the St. Pierre

Bank (Templeman and Bishop 1979), Grand Bank (Templeman et al. 1978), and Georges Bank stocks (Clark 1959; Clark et al. 1982; Overholtz 1987). Lower lengths at 50% maturity in haddock have been associated with slower growth (Raitt 1933; Clark 1959). Density-dependent effects on growth and length at maturity, for example, due to large year classes, have been proposed by Templeman and Bishop (1979) and Templeman et al. (1978). This apparent density-dependent effect is consistent with our findings (Fig. 14). The absence of differences in length at maturity among different areas within NAFO division 4X is further evidence that the stock is homogeneous. It also indicates that length at maturity estimations would be relatively insensitive to variation in sampling coverage within the stock range.

Fecundity

It is difficult to compare fecundity/size relationships among studies because numerous factors may affect the fecundity estimates. These include differences in the physical analysis (e.g. gravimetric versus volumetric) measures of length or weight used and statistical analysis. Often, details of the sampling and analyses are not included or incomplete. It is also noted that, in haddock, fecundity-at-length may be influenced by parasitism (Hislop and Shanks 1979), maturation rate (Sonina 1973), availability of food during the period of gonad maturation (Hislop et al. 1978), and interannual variation (Sonina 1971). Several studies on haddock fecundity have been published (Fig. 16), and our fecundity/length relationship for southwest Scotian Shelf haddock lies within the bounds of the other stocks.

No interannual variation in fecundity at length or weight was observed in this study. Similarly, Hislop and Shanks (1979) found no significant difference in fecundity at length of North Sea haddock either during the period 1976–78 or when these data were compared with those of Raitt (1933). Based on histological examination, Robb (1982) concluded that fecundity was adjusted by the resorption of unshed ova after vitellogenesis. Since fecundity estimates could include eggs destined to be resorbed, the procedure may both overestimate fertility (actual eggs shed) and be insensitive to adjustments in fecundity. Another explanation for the lack of interannual differences in fecundity at length is the observation that the period over which our haddock were sampled was characterized by a very stable population biomass and low variability in growth (O'Boyle and Wallace 1987).

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References

ALEKSEYEVA YE I., AND I. D. TORMOSOVA. 1980. Maturation, spawning and fecundity of the North Sea haddock, *Melanogrammus aeglefinus*. J. Ichthyol. (Engl. Transl. Vopr. Ikhtiol) 19 (2): 56–64.

BAGENAL, T. B. 1978. Aspects of fish fecundity, p. 75–101. *In* S. D. Gerking, [ed.] Ecology of freshwater fish production. John Wiley and Sons. Chap. 4 Blackwell Scientific Publications.

BEACHAM, T. D. 1983. Variability in size and age at sexual maturity of haddock (*Melanogrammus aeglefinus*) on the Scotian Shelf in the Northwest Atlantic Ocean. Can. Tech. Rep. Fish. Aquat. Sci. No. 1168: 32 p.

BERGSTAD, O. A., T. JORGENSEN, AND O. DRAGESUND. 1987. Life history and ecology of the Gadoid resources of the Barents Sea. Fish. Res. 5: 119–161.

BLACKER, R. W. 1971. Synopsis of biological data on haddock *Melanogrammus aeglefinus* (Linnaeus) 1758. FAO Fish. Synop. No. 84.

CAMPANA, S. E., S. J. SMITH, AND P. C. F. HURLEY. 1989. A drift–retention dichotomy for larval haddock (*Melanogrammus aeglefinus*) spawned on Browns Bank. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1): (This issue).

CLARK, J. R. 1959. Sexual maturity of haddock. Trans. Am. Fish. Soc. 88: 212–213.

CLARK, S. H., W. J. OVERHOLTZ, AND R. C. HENNEMUTH. 1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northw. Atl. Fish. Sci. 3: 1–27.

COLTON, J. B., JR. 1965. The distribution and behaviour of pelagic and early stages of haddock in relation to sampling techniques. Spec. Publ. Int. Comm. Nortw. Fish., No. 5: 110–129.

1968. A comparison of current and long-term temperatures of Continental Shelf waters, Nova Scotia to Long Island. Res. Bull. Int. Comm. Northw. Atlant. Fish., No. 5: 110–129.

DEVLAMING, V. L., G. GROSSMAN, AND F. CHAPMAN. 1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A: 31–39.

DRAPEAU, G., AND L. H. KING. 1972. Surficial geology of the Yarmouth–Browns Bank map area. Marine Science Paper 2; Geological Survey of Canada Paper 72–24.

FADER, G. B., L. H. KING, AND B. MACLEAN. 1977. Surfical geology of the eastern Gulf of Maine and Bay of Fundy. Marine Sciences Paper 19; Geological Survey of Canada Paper 76-17.

FANNING, L. P. 1985. Intercalibration of research survey results obtained by different vessels. CAFSAC Res. Doc. 85/03.

FINNEY, D. J. 1971. Probit analysis. Cambridge. Cambridge University Press.

FRANK, K. T., F. H. PAGE, AND J. K. MCRUER. 1989. Hydrographic effects on the vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae on the southwestern Scotian Shelf. Can. J. Fish. Aquat. Sci. 46 (Suppl.1): (This issue).

HALLIDAY, R. G. 1987. Size and age at sexual maturity of Atlantic argentine, *Argentinia silus*: a critique. Environ. Biol. Fish. 19(2): 139–147.

1988. Use of seasonal spawning area closures in the management of haddock fisheries in the Northwest Atlantic. NAFO Sci. Coun. Stud. 12: 27–36.

HALLIDAY, R. G., AND P. A. KOELLER. 1981. A history of Canadian groundfish surveys and data usage in ICNAF Divisions 4TVWX: 273 p. *In* W. G. Doubleday and D. Rivard [ed.] Bottom trawl surveys. Can. Spec. Publ. Fish. Aquat. Sci. No. 58.

HAWKINS, D., K. J. CHAPMAN, AND D. J. SYMONDS. 1967. Spawning of haddock in captivity. Nature (Lond.) 215: 923–925.

HISLOP, J. R. G., A. P. ROBB, AND J. A. GAULD. 1978. Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish Biol. 13: 85–98.

HISLOP, J. R. G., AND A. M. SHANKS. 1979. Recent investigations on the reproductive biology of the haddock, *Melanogrammus aeglefinus*, of the northern North Sea and the effects on fecundity of infection with the copepod parasite *Lernaeocera branchialis*. J. Cons. Int. Explor. Mer 39: 244–251.

HODDER, V. M. 1963. Fecundity of Grand Banks haddock. J. Fish. Res. Board Can. 20(6): 1465–1487.

1965. The possible effects of temperature on the fecundity of Grand Bank haddock. ICNAF Spec. Publ. No. 6. 515–522.

HOMANS, R. E. S., AND V. D. VLADYKOV. 1954. Relation between feeding and the sexual cycle of the haddock. J. Fish. Res. Board Can. 11(5): 535–542.

HTUN-HAN, M. 1978. The reproductive biology of dab *Limanda limanda* (L.) in the North Sea: seasonal changes in the ovary. J. Fish Biol. 13: 351–359.

HURLEY, P. C. F., AND S. E. CAMPANA. 1989. Distribution and abundance of gadid eggs and larvae on the Southwest Scotian Shelf. Can. J. Fish. Aquat. Sci. 46 (Suppl.1): (This issue).

KOHLER, K. 1959. The growth, length–weight relationship, and maturity of haddock (*Melanogrammus aeglefinus* L.) from the region of Lockeport, N.S. J. Fish. Res. Board Can. 17 (1): 41–60.

Marak, R. R., and R. Livingstone. 1970. Spawning dates of Georges Bank haddock. ICNAF Res. Bull. 7: 56–58.

O'Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann, and A. C. Kohler. 1984. Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiological features. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 183: 27–40.

O'Boyle, R., and D. Wallace. 1987. An evaluation of the population dynamics of 4X haddock during 1962–87 with yield projected to 1988. CAFSAC Res. Doc. 87/97.

Overholtz, W. J. 1987. Factors relating to the reproductive biology of Georges Bank haddock (*Melanogrammus aeglefinus*) in 1977–83. J. Northw. Atl. Fish. Sci. 7: 145–154.

Page, F., and K. Frank. 1989. Spawning time and egg stage durations in haddock stocks of the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 46 (Suppl.1): (This issue).

Page, F. H., K. T. Frank, and K. Thompson. 1989. Stage dependent vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs in a stratified water column: field evidence and an interpretive model. Can. J. Fish. Aquat. Sci. 46 (Suppl.1): (This issue).

Powles, P. M. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarias* L.) in the southwestern Gulf of St. Lawrence. J. Fish. Res. Board Can. 15: 1383–1402.

Raitt, D. S. 1933. The fecundity of the haddock. Fish. Board for Scotland Sci. Invest. 1932 No. I. 42 p.

Robb, A. P. 1982. Histological observations on the reproductive biology of haddock, (*Melanogrammus aeglefinus* L.). J. Fish Biol. 20: 397–408.

Roff, D. A. 1983. An allocation model of growth and reproduction in fish. Can. J. Fish. Aquat. Sci. 40: 1395–1404.

Rojo, A. 1955. In summaries of research 1955 — A. Summaries by country — VIII. Spanish Res. Rep. 1955 — B. Researches on the haddock stock in subarea 3. ICNAF Ann. Proceed. Vol. 6 58–63.

Scott, J. S. 1983. Inferred spawning areas and seasons of groundfishes on the Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. No. 1219.

Simpson, A. C. 1951. The fecundity of the plaice. Min. Agric. Fish. Invest. Ser. 11.17(5): 1–27.

Smith, P. C. 1983. The mean and seasonal circulation off southwest Nova Scotia. J. Phys. Oceanogr. 13: 1034–1054.

Smith, P. C. 1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46 (Suppl.1): (This issue).

Sonina, M. A. 1971. La fecondite de l'eglefin Arcto-Norvegien (*Melanogrammus aeglefinus* (Linne)). ICES Demersal Fish Committee C.M. 1971/F:16.

Sonina, M. A. 1973. Peculiarities of the fecundity dynamics of the Arcto-Norwegian haddock (*Melanogrammus aeglefinus* (Linne)). ICES Demersal Fish Committee C.M. 1973/F:13.

Templeman, H., V. M. Hodder, and R. Wells. 1978. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, on the southern Grand Bank. ICNAF Res. Bull. No. 13: 53–65.

Templeman, W., and C. A. Bishop. 1979. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of St. Pierre Bank. ICNAF Res. Bull. No. 14: 77–83.

Wiborg, K. F. 1951. The whirling vessel an apparatus for the fractioning of plankton samples. Fiskeridirektoratets Skifter (Rpt. on Norwegian Fishery and Mar. Invest.) Vol. IX No. 13.

Survival and Abundance of Young Atlantic Cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*) as Indicators of Year-class Strength[1]

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To identify the life history stage(s) most influential in determining yearclass strength, we constructed and analyzed survival curves of the 1983, 1984, and 1985 cohorts of cod and haddock off Southwest Nova Scotia relative to their physical and biological environment. Relative abundance of each Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) yearclass was not reflected by egg or larval abundance in any year examined. However, abundance of both pelagic and settled juveniles did appear to reflect yearclass strength. Egg and larval mortality could not be consistently linked with advection from the spawning site, and did not covary with subsequent recruitment. In both species, mortality between the larval and juvenile stage was inversely correlated with yearclass strength, but sources of the mortality could not be identified. Larval growth was inversely related to mortality of the early larval stage and independent of larval abundance. However, juvenile growth was proportional to mortality and inversely related to abundance. Despite early life coexistence and similarities in spawning time and location, the relative yearclass strengths of cod and haddock in Southwest Nova Scotia were different, suggesting that the timing of local physical and biological events may play an important role in the recruitment success of these stocks.

Pour repérer les stades du cycle biologique qui ont la plus grande influence sur l'effectif des classes annuelles, nous avons établi et analysé les courbes de survie des cohortes 1983, 1984, et 1985 de la morue franche (*Gadus morhua*) et de l'aiglefin (*Melanogrammus aeglefinus*) au sud-ouest de la Nouvelle-Écosse par rapport à leur environnement physique et biologique. L'abondance relative de chaque classe annuelle de morue et d'aiglefin ne concordait avec l'abondance des oeufs ou des larves pour aucune des années examinées. L'abondance des juvéniles aux stades pélagiques et benthiques semblait par contre en rapport avec l'effectif des classes annuelles. La mortalité des oeufs et des larves n'a pas pu être liée de façon conséquente avec l'advection par rapport aux frayères, et ne covariait pas avec le recrutement subséquent. Chez les deux espèces, la mortalité entre les stades larvaire et juvénile était en corrélation inverse avec l'effectif des classes annuelles, mais les sources de mortalité n'ont pu être repérées. La croissance larvaire était inversement liée à la mortalité des premiers stades larvaires et indépendante de l'abondance des larves. Par contre, la croissance au stade juvénile était proportionnelle à la mortalité et inversement proportionnelle à l'abondance. Malgré leur coexistence aux premiers stades de la vie et des similarités dans le moment et le lieu de la ponte, l'effectif relatif des classes annuelles de morue et d'aiglefin au sud-ouest de la Nouvelle-Écosse présentait des différences, qui semblent indiquer que l'avènement de phénomènes physiques et biologiques à l'échelle locale peut jouer un rôle important dans le succès de recrutement de ces stocks.

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There are few fish stocks for which a consensus has been reached concerning the mechanisms and life history stages most influential in the determination of yearclass strength. The complexity of the problem is typified by the wide variety of conclusions reached in recent research on the recruitment of pelagic spawners, such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). While most workers now believe that yearclass strength is determined in the first year of life (Gulland 1965; Cushing 1972; Dickson et al. 1974; Grosslein and Hennemuth 1973; Houde 1987; but see Daan 1987), "key" life history stages have variously been identified as that of egg production (Cook and Armstrong 1986; Rice and Evans 1986), early larval life (Hjort 1914; Corlett 1965; Dickson et al. 1974; Crecco and Savoy 1984), the entire larval stage (Cushing 1972; Jones 1973; Methot 1983; Flierl and Wroblewski 1985; Koslow et al. 1987), the postlarval stage (Lett et al. 1975; Sissenwine et al. 1984; Babcock Hollowed et al. 1987), the pelagic juvenile stage (Peterman et al. 1988; Savoy and Crecco 1988), and that of settled juveniles (Shulman and Ogden 1987; Townsend and Cammen 1988). The list of proposed "key" mechanisms includes, either individually or in combination, advective losses, starvation, predation, and developmental/growth rate, variously modified by density-dependent and/or density-independent factors (e.g. Jones 1973; Cushing 1981; Shepherd and Cushing 1981; Sissenwine et al. 1984; Peterman et al. 1988; Savoy and Crecco 1988; review by Anderson 1988). One conclusion that can be drawn from the above is that no one mechanism or life history stage is likely to be identified as the explanatory factor in all studies of recruitment.

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While some excellent conceptual frameworks now exist for the analysis of recruitment dynamics (Sissenwine 1984; Houde 1987; Miller et al. 1988; Sinclair and Iles 1988), few have been tested through adequate sampling of individual cohorts (yearclasses) at multiple life history stages. Gulland (1965) first suggested the preparation of cohort survival curves based on field survey data as the only definitive test of a recruitment hypothesis. Survival curves (or their equivalent, life stage tables) (Dahlberg 1979) have since been used to advantage by a number of workers, but have generally been either incomplete (Sissenwine et al. 1984; Babcock Hollowed et al. 1987) or restricted to examination of the egg and larval stages (Harding and Talbot 1973; Bannister et al. 1974; Ellertsen et al. 1986; Peterman et al. 1988). Recently, Sundby et al. (1989) developed a multiple stage survival curve for cod off the Norwegian coast, but they were limited to a single survey per year for each stage. Thus, Gulland's (1965) original insight has not yet been fully realized.

Intensive sampling of the cod and haddock populations off Southwest Nova Scotia during the Fisheries Ecology Program (FEP) facilitated the development of cod and haddock survival curves for the years 1983–85. Estimates of absolute abundance were available for the number of spawners and their egg production, as well as several of the stages of developing eggs, larvae, pelagic juveniles, and age-1 recruits. The objective of the survival curve analysis was to identify the life history stage(s) most influential in the determination of yearclass strength. In doing so, we assess the utility of abundance measures at each life history stage as indicators of yearclass strength. In addition, stage-specific mortality rates were calculated for each year and comparisons made both between years and species. Since environmental variables would be expected to influence the trajectory of the curve between stages, interannual and interspecific differences in curve trajectories were interpreted in light of interannual differences in environmental conditions reported in other FEP papers.

Data Preparation and Analysis

The central product of the analysis was a set of survival curves for each of three cohorts (1983–85) of cod and haddock. The survival curves spanned a 1-yr period, from the point just prior to spawning (population fecundity) to beginning-of-year age 1 (cohort analysis). Abundance estimates for intermediate life history stages, including Stage 1 eggs, Stage 4 eggs, larvae, and pelagic juveniles, were derived from stage-specific research surveys. All survey station density estimates were converted to estimates of absolute abundance.

Population Egg Production

Estimates of population fecundity were calculated from published length–fecundity relationships and current estimates of population size. Length–fecundity, rather than age–fecundity relationships were used, since the former are less affected by year-to-year changes in growth rate, and in haddock at least, are considerably more precise (Waiwood and Buzeta 1989). The length–fecundity relationship for haddock (Waiwood and Buzeta 1989) did not differ significantly among the years 1983–86, so the aggregated relationship was used here:

$$\text{Log fecundity} = 0.3456 + 3.1225\ (\text{Log length})$$

Since the fecundity of cod in Southwest Nova Scotia has not yet been determined, the relationship for cod in the Gulf of St. Lawrence (Buzeta and Waiwood 1982) was applied:

$$\text{Log fecundity} = -0.16749 + 3.28\ (\text{Log length})$$

The application of the Gulf fecundity relationship to these data was deemed appropriate because the length–fecundity relationships for cod in other regions differ very little among themselves (Powles 1958; May 1967; Buzeta and Waiwood 1982), and the maturation schedule for cod in the Gulf of St. Lawrence is very similar to that of Southwest Nova Scotia (Holdway and Beamish 1985).

Length-structured estimates of population abundance were calculated as per Campana (1987) using the most recent stock assessments for 4X cod (Campana and Hamel 1989) and 4X haddock (O'Boyle et al. 1989). Beginning-of-year population numbers at age (N_0) were adjusted for mortality between January 1 and the assumed spawning date with the equation:

$$N_t = N_0\exp(-(F+M)t)$$

where F = fishing mortality (yr^{-1}), M = natural mortality (assumed to equal 0.2 yr^{-1}), and t = (DOY of spawning/365) yr. Spawning dates were assessed in relation to the mean weighted date of Stage 1 egg production, and set to Day 97 for haddock and Days 73, 90, and 90 for cod in 1983, 1984, and 1985, respectively. Size-at-age in the population was calculated from research vessel age–length keys for the years 1983–85, weighted appropriately by length frequency.

Survey Calculations

Ichthyoplankton surveys were conducted at roughly monthly intervals between February and June of 1983–85 (Hurley and Campana 1989). To ensure uniform coverage of the survey grid across years, only those stations common to most surveys and representative of the cod and haddock populations were examined (Fig. 1) (Hurley and Campana 1989). Stations on Georges Bank were not included in the analysis. All station estimates of abundance were converted to numbers per square metre. The sampling emphasis on and around Browns Bank (Fig. 1) could have biased the subsequent estimates of absolute abundance. Therefore, the mean abundance estimate for all Browns Bank stations was calculated from the high-density station grid and reweighted according to the sampling density in the remainder of the survey grid. Finally, a single estimate of mean cruise

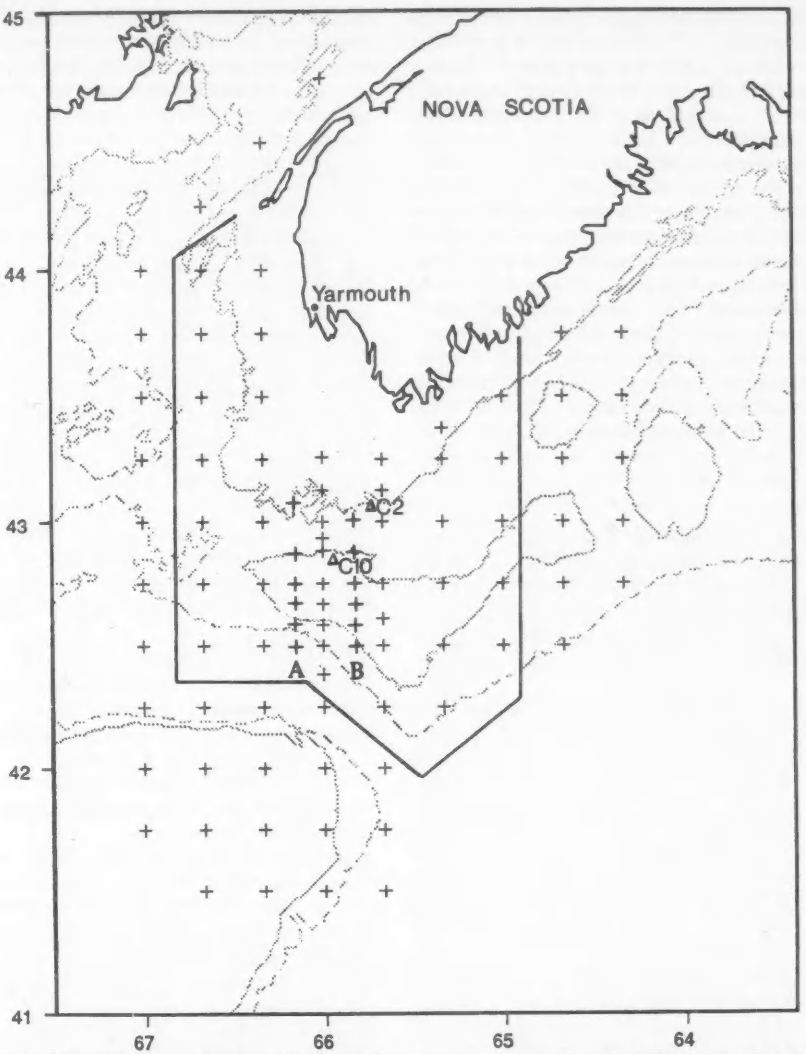

FIG. 1. Map of study area showing collection stations, current meter mooring sites (C2, C10), and wind recording site (Yarmouth). The solid line delineates those stations used in the abundance calculations. Transects A and B were not sampled in 1983.

number per square metre was calculated for each life history stage.

Pelagic juvenile surveys were conducted over the same grid as that described above (Fig. 1), using stations common to the ichthyoplankton survey and the methodology described in Koeller et al. (1986). While the 1983 survey employed oblique tows to within 5 m of the bottom, the 1984 and 1985 surveys were restricted to the upper 60 m of the water column. The vertical distribution of pelagic haddock juveniles is well suited to a depth-restricted survey (Koeller et al. 1986). However, cod juveniles may be found below 60 m (Koeller et al. 1986), implying that the survey may have underestimated their abundance in 1984 and 1985.

Species Identification

All of the cod and haddock life history stages were readily identifiable to species, with the exception of the early stage eggs (Hurley and Campana 1989). Stage 1 cod–haddock–witch (witch flounder, *Glyptocephalus cynoglossus*) (CHW) eggs were subsequently assigned to species through use of a linear interpolation procedure. Classification difficulties prevented any further breakdown of CHW Stages 2 and 3. The species-assignment procedure was based upon the known species composition of the Stage 4 eggs (late stage) in the same and subsequent cruises, assuming a linear gradient in relative proportions between the two cruises. Position along the gradient was assigned on the basis of the duration of the egg stage and the time interval between cruises. The species segregation procedure was limited to two species at one time as witch eggs were not present before June, and cod eggs were not present in significant quantities after May. For cod, the following algorithm was used:

$$C_{t1} = \mathrm{CHW}_{t1} \times (P_{t1}+((D\times(t_2-t_1)^{-1}) \times (P_{t2}-P_{t1})))$$

where C = the mean number of cod eggs, t_1 and t_2 are the days of the year for cruises 1 and 2, D = stage duration from Stage 1 to the beginning of Stage 4, and P = proportion of Stage 4 cod eggs relative to stage 4 cod and haddock eggs combined. Stage durations were calculated from the individual stage regression equations of Page and Frank (1989), using development temperatures observed at Station C10 (Fig. 1) at a depth of 15 m on the appropriate date (Lively 1989; Smith 1989a). For all cruises prior to June, Stage 1 haddock egg abundance was calculated as the difference between C_{t1} and CHW_{t1}. CHW abundances could not be decomposed in the manner described above for the last cruise of each year (June); accordingly, haddock:witch egg abundance at Stage 1 was linearly extrapolated using the proportions of Stage 4 haddock:witch eggs in the same and previous cruises. Given the later spawning time of witch flounder relative to haddock (Neilson et al. 1988), this assumption, although unavoidable, almost certainly resulted in an overestimate of Stage 1 haddock egg abundance in each of the June cruises.

Annual Production

Virtually all of the ichthyoplankton production by cod and haddock was encompassed by the five monthly surveys. To estimate the absolute annual production (in numbers) of each life history stage, the area under the curve depicting the monthly time series of mean stage abundance was first integrated, then divided by the stage duration, and finally multiplied by the area of the survey grid.

Time series curves of abundance for each stage and year were prepared by plotting the mean cruise abundance on the median date of each cruise. Only cod and haddock larvae and late-stage haddock eggs in 1984 appear to have had any significant production after the last (June) cruise. For those stages, production was assumed to have peaked in June 1984, and declined linearly to zero by Day 198. This assumption was supported by the results of an independent ichthyoplankton survey of Browns Bank in July 1984 (see Results). With the exception of the cases listed above, production of all stages was assumed to have been initiated on Day 30 and ended by Day 170.

Egg stage durations were calculated as described previously. In theory, the duration of the larval stage extended to that of the juvenile stage. In practice however, larval catchability by the bongo gear, relative to a comparable sampling device, declined substantially at lengths exceeding 10 mm (Suthers and Frank 1989). Mean larval ages at 10 mm were approximated using observed ambient temperatures and 10% preservation shrinkage (Fowler and Smith 1983) in the age–temperature growth model of Campana and Hurley (1989). Therefore, the effective catchable duration was calculated as 42, 42, and 46 d for cod larvae, and 55, 45, and 47 d for haddock larvae, in 1983–85, respectively. Given the relatively long expected duration of the pelagic juvenile stage (Suthers et al. 1989), the annual juvenile midwater trawl survey could reasonably be expected to have sampled the entire year's production. The resulting estimate of juvenile abundance assumed that the pelagic survey occurred after peak larval production, and before the transformation to a demersal lifestyle (Koeller et al. 1986). This assumption appeared to be reasonable in 1983 and 1985, but was probably invalid in 1984 (see Results).

Estimates of absolute abundance were derived by integrating under the annual production curve for each life history stage, followed by division by the stage durations described earlier. Absolute abundance was then calculated by multiplying the resulting mean annual station abundance (number per square metre) by the area encompassed by the population. The latter was taken to include both the survey grid and the unsampled region between the Nova Scotia coastline and the northernmost boundary of the survey grid, resulting in an overall population area of $3.193 \times 10^{10} \mathrm{m}^2$. The assumption that the unsampled region was characterized by ichthyoplankton abundances similar to those in the survey grid could not be rigorously tested, but seemed reasonable in light of independent surveys (Suthers and Frank 1989). Given the relatively small water volume in the unsampled region, moderate departures from this assumption would not alter the conclusions of this study.

Estimates of absolute abundance at an age of 1 yr were derived from the most recent stock assessments (Campana and Hamel 1989; O'Boyle et al. 1989). While sensitive to the input value of M and the most recent estimate of F, population estimates for the 1983–85 cohorts should be reasonably stable, with stability increasing for the earlier cohorts.

Survival curves were prepared by plotting the annual production estimate for each life history stage versus the mean weighted day of occurrence. Since the mean weighted date for 1983 cod larva production was influenced by the abundance of large, fall-spawned larvae early in the year (Fig. 2), the date was set to a value 42 d later than that of Stage 4 egg production.

Mortality Calculations

We considered two alternative means of estimating instantaneous mortality rates between life history stages. Although both were based upon the standard equation,

$$M = \ln (N_1/N_0) \times (t_1 - t_0)^{-1}$$

where N_0 and N_1 are the absolute annual abundances of two sequential life history stages, the two estimation procedures employed different calculations for the time interval $(t_1 - t_0)$ between the stages. Mortality calculations where the interval was set to the difference between the mean weighted dates of the two life history stages produced qualitatively similar, but somewhat higher, values than those where $t_1 - t_0$ was based upon the expected interval between stages (as described previously). In a series of calculations with simulated data and age-structured mortality, both approaches produced accurate estimates of mortality when stage-specific mortality rates were independent of date, and biased estimates when mortality varied with both stage and date. Since the calculations based upon mean weighted dates were slightly less accurate in the presence of date-specific mortalities, mortality rates were calculated using expected interstage intervals. However, mean weighted dates were used for the larval-juvenile interval, since the expected interval was unknown.

Oceanographic Conditions

As a measure of the relative differences in oceanographic conditions among the years 1983–85, the low-passed data from the long-term mooring (C2; Fig. 1) on the inshore 100-m isobath off Cape Sable (Lively 1989; Smith 1989a) were taken to be representative of the entire Southwest Nova Scotia region. Smith (1989b) used a multiple regression technique in the extraction of significant annual cycles from monthly mean C2 data and other meteorological variables, such as Yarmouth wind stress, to demonstrate various correlations among the anomalies (residuals) from the annual cycle. Longshore wind stress anomalies were associated with deep longshore advection on the shelf which resulted in the transport of warm, salty (cold, fresh) water into the region from the Gulf of Maine (Scotian Shelf) when the wind was directed to the northwest (southeast).

Advection Model

Estimates of the direction and magnitude of ichthyoplankton displacement from Browns Bank were made with the tide- and wind-driven circulation model of Page and Smith (1989). For the western cap of Browns Bank, the model calculations appeared to be qualitatively correct in terms of direction and relative displacement magnitude, although they significantly underestimated the observed displacement of near-surface drogues. On the other hand, model calculations were inadequate for predictions of displacement on the eastern portion of the Bank i.e. — in one case, the model displacement was in the opposite direction from that observed. Therefore, the results presented here will only be interpreted qualitatively and in the context of displacement from the western cap of Browns Bank.

Advection and dispersion of eggs was simulated by seeding a particle onto the cap of Browns Bank on the mean weighted date of egg production (both Stages 1 and 4) for each species and year. The particle trajectories were then calculated over an integral number of M_2 cycles until the beginning of the subsequent life history stage. Surface wind stress forcing, assumed to be uniform over the region, was based on smoothed (66-h running mean) estimates from Sable Island (Smith 1989a). Single model particles were deemed to be representative of the entire displacement field for a given species and stage on the basis of the relative uniformity of particle trajectories on the bank under tidal and wind forcing (Page and Smith 1989). Interannual differences in net displacement were then interpreted in relation to the estimated mortality rate for that life history stage.

Results

Abundance and Survival

The date of peak cod spawning appeared to differ by less than 2 wk among years, as indicated by the production of Stage 1 eggs (Fig. 2). Differences in timing became more apparent in the Stage 4 and larval production curves, with the 1984 cohort lagging behind the others. Interannual differences in the abundance of each stage were first evident at Stage 1, but became progressively more pronounced with time. In particular, the abundance of the 1984 cohort decreased from a level similar to that of the 1985 cohort at Stage 1, to approximately one-tenth its size at the larval stage. In general, the annual pulse of egg and larval production was well defined by the surveys; although the 1984 larval production peaked in June, a subsequent independent survey of Browns Bank between July 16–22, 1984 (Days 197–203), collected no Stage 4 cod eggs or larvae (K. Frank, unpubl. data).

The annual production cycle of haddock eggs and larvae (Fig. 2) differed both with respect to timing and relative cohort abundance compared with that of cod. Spawning occurred 5–30 d after cod in each year. Stage 1 egg production in 1984 lagged 2–3 wk behind that of the other years, with the timing difference persisting through other stages and increasing with time. Cohort strengths at Stage 1 were roughly similar among years, although 1983 larval production was one to two orders of magnitude less than that of the other years. The relative decline in abundance of the 1983 yearclass was clearly evident by egg Stage 4. Larval production was not circumscribed by the surveys in 1984 and 1985, nor was Stage 4 egg production in 1984; however, an independent survey of Browns Bank between July 16–22, 1984 (Days 197–203), collected few Stage 4 haddock eggs (0.01148 per m^2) and larvae (0.02797 per m^2) (K. Frank, unpubl. data), indicating that egg and larval production probably peaked before the last survey of each year.

Coefficients of variation for each of the survey estimates of stage abundance are presented in Table 1. The mean coefficient of variation over all stages and cruises was 285%, corresponding to a confidence interval of about 89% of the mean. The relative size of the confidence interval decreased with increased abundance. Since the variance estimates were calculated under the assumption that all stations were random and independent, and since the variance increased with the mean, the coefficients of variation in Table 1 are almost certainly overestimated.

The absolute abundance of each cohort decreased five to seven orders of magnitude in the first year of life for both species; virtually all of the decline occurred prior to the pelagic juvenile stage (Fig. 3). Considering the range in abundance that was spanned, the similarities in abundance at the age of recruitment (age 1), both between and within species, were noteworthy. However, there were large differences in abundance at intermediate life history stages. Indeed, intraspecific and interannual variability at these stages was considerably larger than at the start or end points of the survival curves.

The egg and larval production of both species was relatively early in 1983 and relatively late in 1984. In the latter, the delayed production was probably responsible for the extremely low estimate of pelagic juvenile haddock abundance, as it resulted in a mean weighted date of larval haddock production that was only 2 d earlier than the midpoint of the juvenile survey.

Interannual differences in survival curve trajectories were best described by instantaneous mortality rates (Fig. 4). On average, the instantaneous mortality rate of both the cod and haddock egg and larval stages was between 0.15–0.30·d^{-1}. While postjuvenile mortality was always much lower, none of the earlier life history stages was consistently associated with particularly high or low mortalities. Substantial interannual differences in mortality rate at each stage were clearly evident, although no one cohort consistently exhibited high or low mortalities across all stages. There were also no consistent interspecific differences in mortality at a given stage.

Exponential growth rates from near the time of hatch to the pelagic juvenile stage indicated that growth varied by as much as a factor of 2.2 between years (Table 2). Independent estimates of growth rate derived from the examination of the otolith microstructure of juveniles (Suthers et al. 1989) were similar to those calculated for the 1985 cod cohort. The cod and haddock growth rates were broadly similar, but did not parallel each other across years.

Oceanographic Conditions

The low-passed time series of C2 temperature (Fig. 5) and salinity (not shown) indicate that the deeper waters off Cape Sable were relatively warm and saline during March and April of 1985 as compared with the more normal conditions in 1983 and 1984. These conditions extended to at least the 70-m isobath on the northern flank of Browns Bank, as indicated by data from other moorings (C3, C10; Smith 1989a). The reason for the relatively warm and saline spring in 1985 may be found in the Yarmouth monthly wind stress anomalies (Fig. 6), which

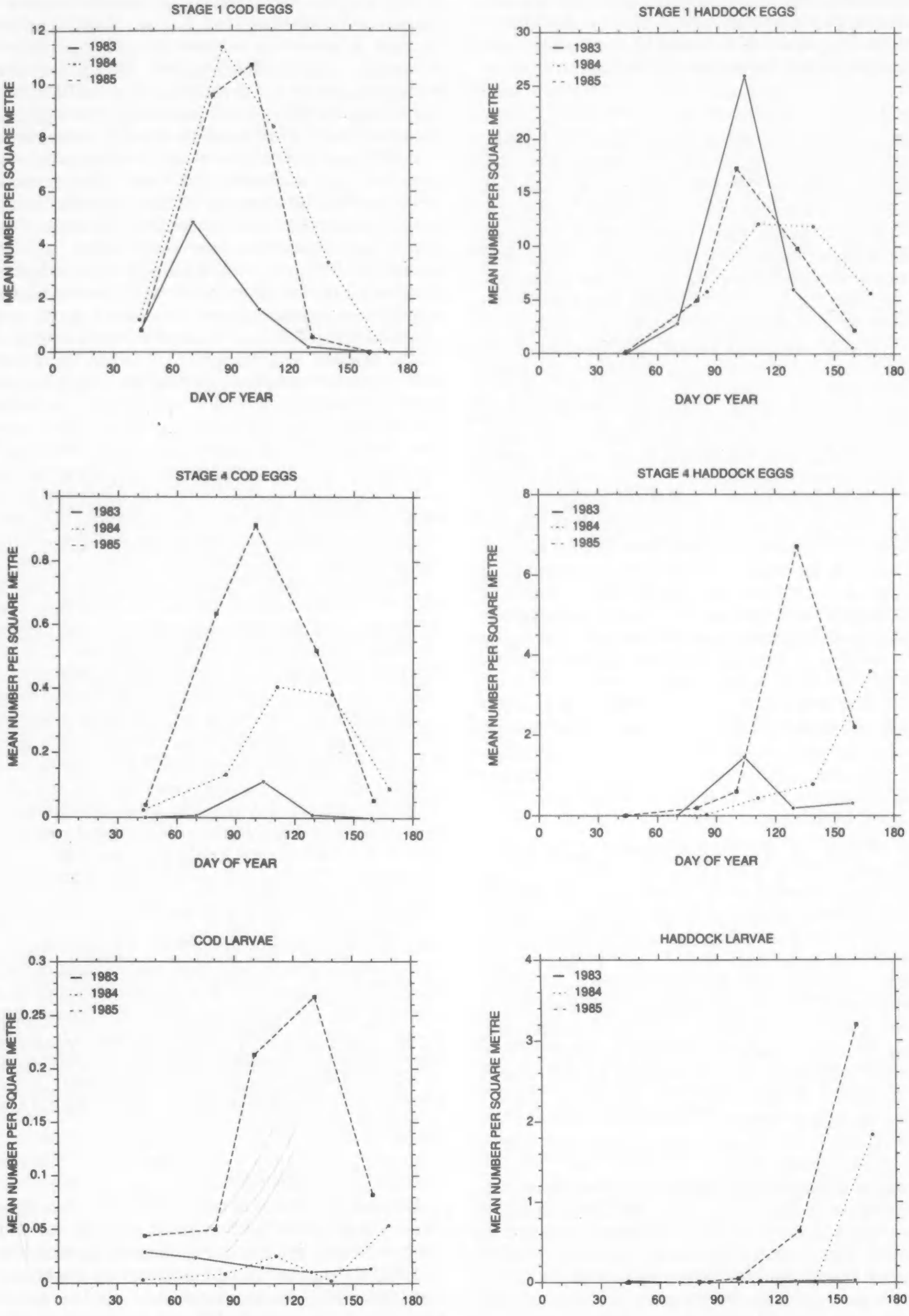

FIG. 2. Annual production cycle of cod and haddock eggs and larvae in Southwest Nova Scotia between 1983–85. An independent survey of Browns Bank in July 1984 indicated that egg and larval abundances were near zero by Day 200.

TABLE 1. Calculated coefficients of variation for each of the stage- and cruise-specific abundance estimates used in the preparation of annual production curves. Actual coefficients are probably smaller than those presented here.

			Coefficient of variation (%)						
Year	Month	Cruise	CHW Stage 1	Cod eggs Stage 4	Cod larvae	Haddock eggs Stage 4	Haddock larvae	Cod juveniles	Haddock juveniles
1983	Feb.	H091	234	—	409	—	574		
	Mar.	H093	252	574	574	—	—		
	Apr.	P288	145	206	529	276	—		
	May	H097	152	632	632	166	444		
	June	H099	147	—	624	239	437		
	June	N011						182	233
1984	Feb.	H112	327	244	453	—	—		
	Mar.	H114	263	269	656	372	—		
	Apr.	H116	132	158	227	322	306		
	May	H118	165	210	714	181	502		
	June	H120	159	326	234	150	153		
	June	N029						376	181
1985	Feb.	H130	228	182	320	558	—		
	Mar.	H132	136	165	185	160	351		
	Apr.	H133	143	175	178	172	189		
	May	H135	147	145	116	129	174		
	June	H137	133	300	176	142	178		
	June	N047/H138						106	253

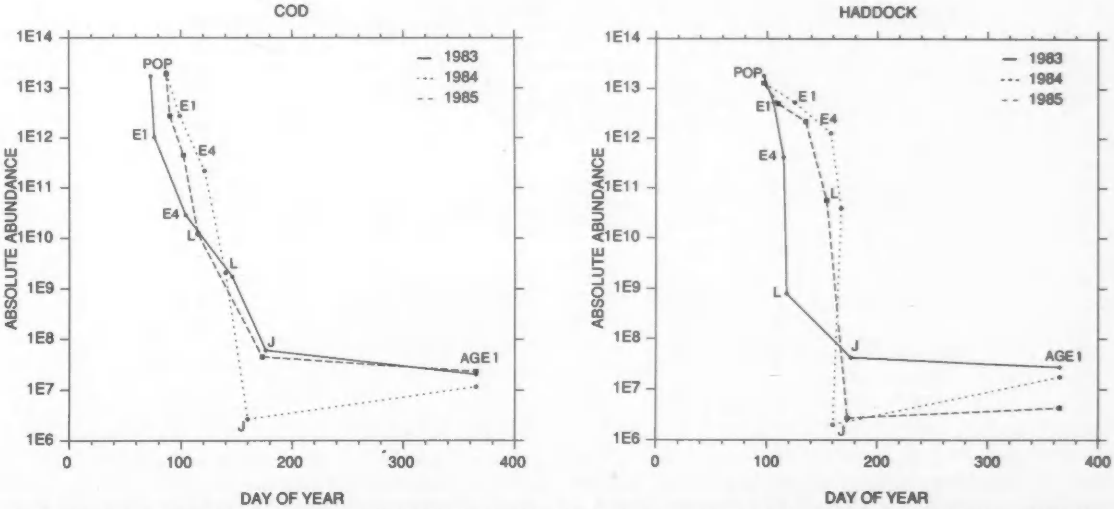

FIG. 3. Survival curves for each of three cohorts (1983–85) of cod and haddock in Southwest Nova Scotia. Estimates of absolute annual abundance (logarithmic scale) for each of the sampled life history stages have been plotted against the corresponding mean weighted date of occurrence. POP = population egg production; E1 = egg Stage 1 (early stage); E4 = egg Stage 4 (late stage); L = larvae; J = pelagic juveniles; AGE 1 = end of first year of life as derived from cohort analysis.

show large, negative longshore stress residuals in February–April of 1983–84, compared with smaller, positive residuals in 1985. The resulting longshore advection anomalies brought either cold, fresh deep water from the Scotian Shelf (negative stress) or warm, salty water from the Gulf of Maine (positive stress) (Smith 1989b). Hence the persistence of strong, longshore winds in April 1984 was associated with the prolonged period of cold temperatures throughout the water column. At depths where most eggs and larvae are found (16–50 m), April–May 1984 was cool, while the corresponding months in 1983 and 1985 were both relatively warm. Of course, temperature effects on the eggs and larvae must also be put into the context of the timing of production; for instance, the timing of 1984 haddock larval production was sufficiently delayed so that the larvae actually experienced warmer temperatures than those of the other years.

Circulation and Advection

The results of the particle-tracking circulation model (Table 3) are generally consistent with inferences made from the Yarmouth monthly wind stress anomalies (Fig. 6), which are them-

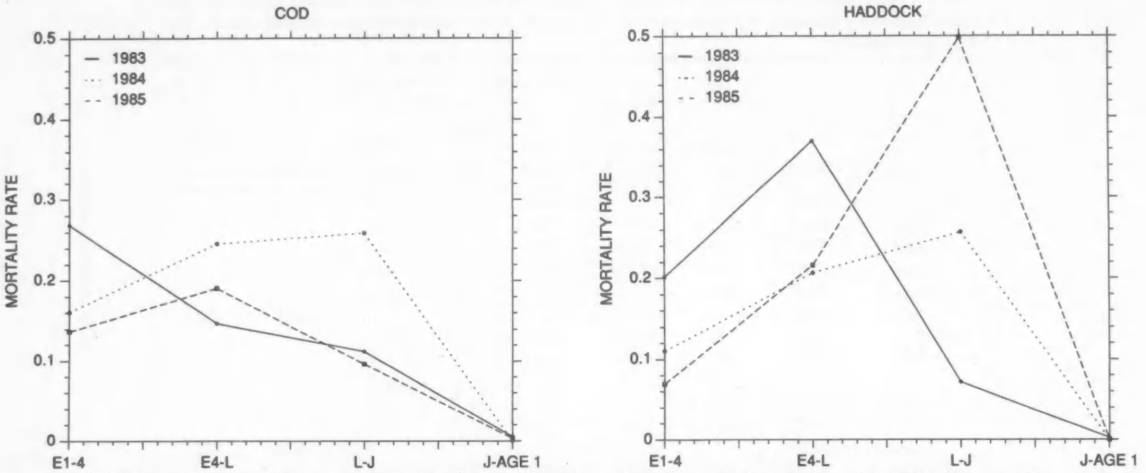

FIG. 4. Daily instantaneous mortality rates between life history stages for each of three cohorts of cod and haddock. E1 = egg Stage 1 (early stage); E4 = egg Stage 4 (late stage); L = larvae; J = pelagic juveniles; AGE 1 = end of first year of life as derived from cohort analysis. Time intervals for the mortality calculations were based on expected life-stage durations.

TABLE 2. Growth rate approximations for young cod and haddock assuming exponential growth, a mean hatch length of 4.0 mm, and a mean hatch date shortly after the mean weighted date of egg Stage 4 production. The growth of the 1984 haddock cohort was not calculated, due to the inappropriate timing of the juvenile survey. DOY = day of year; — = insufficient data.

	Cod			Haddock		
	1983	1984	1985	1983	1984	1985
Egg 4 DOY	104	121	102	115	168	135
May larvae						
DOY	—	125	135	—	—	135
Length (mm)	—	8.00	8.40	—	—	4.32
N	—	4	130	—	—	123
Juvenile						
DOY	176	160	173	176	160	173
Length (mm)	40.8	44.7	28.5	43.7	31.3	38.4
N	233	6	120	168	12	16
Instantaneous growth rate (d^{-1})						
Egg 4 – Larvae	—	—	0.0225	—	—	—
Egg 4 – Juvenile	0.0323	0.0619	0.0282	0.0392	—	0.0595
Larvae – Juvenile	—	—	0.0328	—	—	0.0575

selves correlated with the Sable Island winds actually used in the trajectory simulations. In April 1984 for example, the strong positive along-shelf wind stress anomaly corresponds with the predicted large displacement of Stage 1 cod eggs to the northwest during DOYs 99–121. The weaker negative along-shelf anomaly in May corresponds with the predicted smaller displacement toward the east during DOYs 125–158. Although some influence of the cross-shelf stress anomalies is also evident in the model displacements, the effects are small since cross-shelf winds are not as effective in driving the circulation as are along-shelf winds (Page and Smith 1989).

The wind patterns and dispersion model results highlight important differences in the circulation during the cod and haddock spawning seasons, as well as differences between years (Table 3; Fig. 6). In all three years (1983–85), the magnitude of the wind stress anomalies and the predicted displacements decreased through the April–May period. The peak abundance of early stage cod eggs occurred just prior to the onset of this decrease, when the anomalies and displacements were often relatively large (>40 km, except in 1985). In contrast, the peak abundance of early stage haddock eggs occurred during the seasonal transition. These differences resulted in unique patterns of predicted early life stage displacement. The early stage cod eggs were displaced large distances off the bank, toward the north or northwest, in 1983 and 1984, and largely retained on the bank in 1985. Early stage haddock egg displacement was more variable, with northwest displacement in 1983, retention on the eastern portion of the bank in 1984, and weak southwestward displacement in 1985. The displacement of late stage eggs and larvae often differed from that of the earlier stages (Table 3).

Discussion

The relative abundance of each of the cod and haddock year-classes was not reflected by spawning stock biomass. Popula-

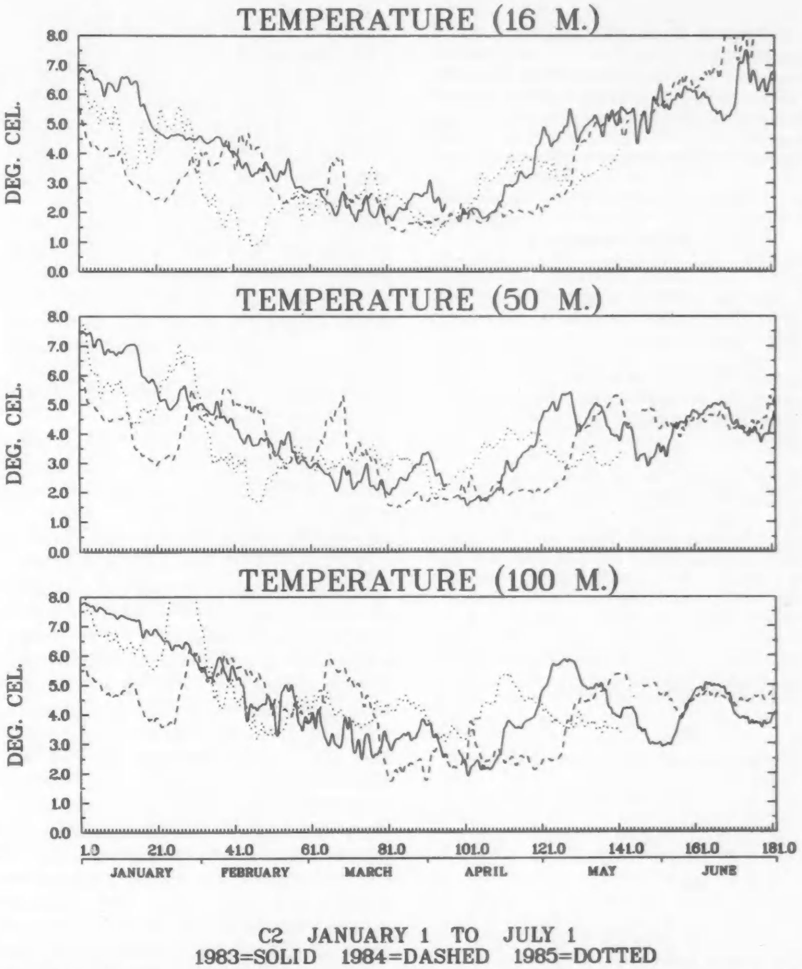

FIG. 5. Low frequency temperature time series at mooring C2. Hourly temperatures were low-pass filtered (half-power point at 31 h) and subsampled at 6-h intervals.

tion egg production varied by less than 30% among years for the two species, while yearclass strength at age-1 differed by up to a factor of six. This result was not surprising, since most workers have been unable to detect a stock–recruitment relationship in either cod or haddock (Gulland 1965; Grosslein and Hennemuth 1973; Jones 1973; Koslow 1984). Of greater interest is the fact that neither egg nor larval abundance could be used to even rank the recruitment levels of cod or haddock, although significant correlations have been reported in other species (Cushing 1972; Brander and Houghton 1982; Leggett et al. 1984; Crecco et al. 1986). While much longer time series were used in the above studies, a rank correlation might have been expected in our data given similar relationships. Indeed, on the basis of extremely low larval abundance, Koslow et al. (1985) predicted recruitment failure for the 1983 yearclass of haddock in Southwest Nova Scotia; that yearclass has since been demonstrated to be only slightly below the long-term mean (O'Boyle et al. 1989). Sampling error cannot account for our results, since the interannual variability in abundance of a given stage was often more than an order of magnitude larger than our sampling error. Substantial changes in ranked abundance even occurred within the egg stage, between Stages 1 and 4. In the absence of appropriate qualifiers (e.g. condition factor; Frank and McRuer 1989), it is difficult to foresee measures of egg or larval abundance being used to predict the yearclass strength of cod or haddock in this region.

While the 1984 juvenile haddock survey was probably an inaccurate reflection of abundance because of the delayed production of the cohort, the abundance of the remaining pelagic juvenile cohorts did appear to reflect subsequent yearclass strength, as has been reported for other populations (Lett et al. 1975; Cook 1984; Randa 1984; Peterman et al. 1988; Sundby et al. 1989). In addition, bottom trawl surveys conducted approximately 1 mo after each of the pelagic juvenile surveys provided similar indices of recruitment success (Campana and Hamel 1989; O'Boyle et al. 1989). Of course, given the cumulative effect of large interannual variations in stage-specific mortality through the early life history, stage-specific recruitment indices would be expected to converge on the final estimate as older stages were sampled. While Koeller et al. (1986)

TABLE 3. Qualitative estimates of the direction and magnitude of advection during the egg and early larval period for cod and haddock between 1983–85. Displacement estimates were based upon the tide- and wind-driven dispersion model of Page and Smith (1989). Start and end points for the calculations are the mean weighted dates of egg production for stages 1 and 4.

			DOY		Displacement	
			Start	End	Direction	Magnitude (km)
1983	Cod	Egg 1	80	104	NW	45
		Egg 4	104	130	NW	38
	Haddock	Egg 1	104	115	NW	38
		Egg 4	115	125	E	14
1984	Cod	Egg 1	99	121	NW	116
		Egg 4	121	140	E	14
	Haddock	Egg 1	125	158	E	43
		Egg 4	158	167	SE	7
1985	Cod	Egg 1	99	102	N	7
		Egg 4	102	120	SE	69
	Haddock	Egg 1	110	135	SW	25
		Egg 4	135	154	SE	11

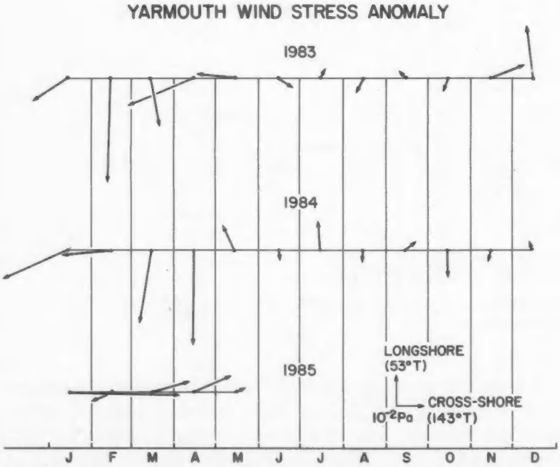

FIG. 6. Monthly mean wind stress anomalies at Yarmouth. Anomalies were computed as deviations from the average annual cycle over the period 1979–85 (Smith 1989b). Positive longshore direction (53°T) is upward.

have outlined the difficulties in using juvenile surveys to obtain unbiased abundance estimates, our results suggest that species-specific refinements in juvenile survey design may have the potential to provide even closer approximations of relative yearclass strength.

Mortality rates up to and including the larval stage were not rank-correlated with yearclass strength, although substantial interannual variations were observed. Similar results have been reported elsewhere (Peterman and Bradford 1987), although a consensus is not yet evident (Gulland 1965; Methot 1983; Savoy and Crecco 1988). In contrast, the mortality rate between the larval and juvenile stage appeared to be inversely related to subsequent yearclass strength. As noted by a number of authors, the mortality rate during the postlarval/juvenile stage would be expected to be an influential modifier of recruitment success, if only because of its duration relative to the other stages (Sissenwine et al. 1984; Houde 1987; Peterman et al. 1988). This was certainly the case in these populations, given mean egg development times of about 16 d (Page and Frank 1989), mean larval ages of about 20 d (Campana and Hurley 1989), and juvenile ages of at least 80 d (Suthers et al. 1989). While the change in cohort abundance during the larval–juvenile stage was not necessarily greater than that of any other stage, our results suggest that the mortality rate during that period resulted in cohort strengths that changed very little over the remainder of the first year of life. Such a conclusion is also in keeping with the observations of relative abundance at the pelagic juvenile and settled juvenile stages.

Advection out of the survey area could not be consistently associated with high mortality rates, although it was the process which might be expected to contribute the most to the mortality of eggs and early larvae. On an annual basis, 1983 advection was predominantly off-bank to the northwest, 1984 featured the largest advective event for a given stage (cod E1-E4), and 1985 was characterized by generally small displacements, indicating retention on the bank, especially for haddock. However, large advection events that occurred at the peak of egg and early larval production could not be consistently identified as significant sources of mortality. While advection off the bank need not necessarily result in mortality (Campana et al. 1989), nearshore waters have been identified as less favourable environments for both late-stage haddock eggs and haddock larvae (Frank and McRuer 1989; Frank et al. 1989). The apparent absence of a relationship between advection and cohort mortality in this study may either reflect inadequacies in the circulation model used to assess advection (Page and Smith 1989), buffering of the local influences of advection by the relatively wide-spread distribution of eggs (Hurley and Campana 1989), or masking by other effects. In any event, it appears that interannual differences in off-bank advection had little effect upon subsequent yearclass strength.

While measures of predator and prey abundance were available to this analysis, their collection was made on a scale that was too coarse to be biologically meaningful (Ellertsen et al. 1984; Fortier and Leggett 1984; Taggart and Frank 1989). On an annual basis, 1985 has been characterized as a year of high primary and secondary production (Koslow et al. 1989). However, this high level of production was not reflected in reduced larval mortality or enhanced yearclass strength of the 1985 haddock cohort, which was among the weakest on record (O'Boyle et al. 1989). Since prey and predator abundance would be expected to influence egg and larval survival, we conclude that annual production estimates are a poor measure of availability, and that characterizations of yearly production as "good" or "bad" (Koslow et al. 1989) are unlikely to aid in the prediction of cod and haddock recruitment.

As a covariate of the major mortality processes, growth rate is widely considered to be an important modifier of early life survival (Houde 1987; Peterman et al. 1988). Both the cod and the haddock larval growth rates (Campana and Hurley 1989), based on observed temperatures after the time of peak late-stage egg production, were inversely related to the observed mortality rates, but appeared to be independent of larval abundance. While tentative, these results are consistent with the conceptual framework linking growth and mortality through its influence on stage duration (Houde 1987; Miller et al. 1988). However, larval growth rate through to the pelagic juvenile stage appeared to influence mortality differently. Postlarval growth in each year and species was proportional to the larval–juvenile mortality rate, and inversely proportional to juvenile abundance. Despite apparent consistency with density-dependent processes, our observations were too few to test previous reports of density-dependent growth and mortality in the juvenile stage (Shepherd and Cushing 1981; Zijlstra et al. 1982). However, our size-at-date data did not serve as useful proxies for yearclass strength.

Broad similarities in the yearclass strengths of sympatric cod and haddock stocks (Martin and Kohler 1965; Templeman 1972; Koslow 1984) suggest that large-scale environmental effects influence recruitment (Koslow 1984; Babcock Hollowed et al. 1987). However, despite the fact that the stocks that we studied experienced the same large-scale effects, the recruitment success of cod and haddock differed in 1984, and was totally divergent in 1985. These recruitment dichotomies can probably be attributed to more local events, such as those due to heterogeneous spatial or temporal effects. For example, consider the interannual comparison of temperatures at mooring C2 (Fig. 5), which represents the temperature field of the local region. On a gross scale, the spring of 1984 could be classified as cooler than that of 1983, primarily because of the prolonged period of cold temperatures in March-April, 1984. Yet, because of the delay in the time of haddock larval production, the ranking of the yearly temperatures to which the larvae were exposed would be reversed. These phasing effects may well be responsible for reported univariate relationships between the environment and yearclass strength in some populations (Martin and Kohler 1965; Dickson et al. 1974; Hansen and Buch 1986) but not in others. Similar arguments can be made with respect to annual assessments of advection and zooplankton production (Koslow et al. 1989), both of which were too coarse as measures to provide consistent explanations for the divergence in cod and haddock survival patterns.

Questions left unanswered by this analysis can be used to suggest avenues for further research. In particular, we recommend further research on the growth, sources of mortality, and susceptibility to oceanographic influences of the juvenile stage. Improvements to the particle dispersion model could be used to compare the observed and expected distribution of ichthyoplankton throughout the spawning season, and thus test more completely the hypothesis that advection is (or is not) an important source of egg and larval mortality. And finally, more work is required to assess the influence of larval condition on subsequent survival. In an applied context, fisheries managers may view these research recommendations as a means of enhancing our ability to predict the strength of upcoming yearclasses.

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References

ANDERSON, J. T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northw. Atl. Fish. Sci. 8: 55–66.

BABCOCK HOLLOWED, A., K. M. BAILEY, AND W. S. WOOSTER. 1987. Patterns in recruitment of marine fishes in the northeast Pacific Ocean. Biol. Oceanogr. 5: 99–131.

BANNISTER, R. C. A., D. HARDING, AND S. J. LOCKWOOD. 1974. Larval mortality and subsequent year-class strength in the plaice (*Pleuronectes platessa* L.), p. 21–37. *In* J. H. S. Blaxter [ed.] The early life history of fishes. Springer-Verlag, NY.

BRANDER, K., AND R. G. HOUGHTON. 1982. Predicting the recruitment of North Sea plaice from egg surveys. ICES C.M. 1982/G: 5.

BUZETA, M.-I., AND K. G. WAIWOOD. 1982. Fecundity of Atlantic cod (*Gadus morhua*) in the southwestern Gulf of St. Lawrence. Can. Tech. Rep. Fish. Aquat. Sci. 1110: iii + 6 p.

CAMPANA, S. E. 1987. Comparison of two length-based indices of abundance in adjacent haddock stocks (*Melanogrammus aeglefinus*) on the Scotian Shelf. J. Cons. Int. Explor. Mer 44: 43–55.

CAMPANA, S., AND J. HAMEL. 1989. Status of the 4X cod stock in 1988. CAFSAC Res. Doc. 89/30.

CAMPANA, S. E., AND P. C. F. HURLEY. 1989. An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 46: 603–613.

CAMPANA, S. E., S. J. SMITH, AND P. C. F. HURLEY. 1989. A drift-retention dichotomy for larval haddock (*Melanogrammus aeglefinus*) spawned on Browns Bank. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

COOK, R. M. 1984. Observations on the international 0-group gadoid survey indices. ICES CM 1984/G: 66

COOK, R. M., AND D. W. ARMSTRONG. 1986. Stock-related effects in the recruitment of North Sea haddock and whiting. J. Cons. Int. Explor. Mer 42: 272–280.

CORLETT, J. 1965. Winds, currents, plankton and the year-class strength of cod in the western Barents Sea. ICNAF Spec. Publ. 6: 373–378.

CRECCO, V. A., AND T. F. SAVOY. 1984. Effects of fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. Can. J. Fish. Aquat. Sci. 41: 1216–1223.

CRECCO, V., T. SAVOY, AND W. WHITWORTH. 1986. Effects of density-dependent and climatic factors on American shad *Alosa sapidissima*, recruitment: a predictive approach. Can. J. Fish. Aquat. Sci. 43: 457–463.

CUSHING, D. H. 1972. The production cycle and the numbers of marine fish. Symp. Zool. Soc. Lond. 29: 213–232.

1981. Stock and recruitment. Chap. 7, p. 376–405. Fisheries biology: a study in population dynamics. Univ. of Wisconsin Press. Madison.

DAAN, N. 1987. Multispecies versus single-species assessment of North Sea fish stocks. Can. J. Fish. Aquat. Sci. 44(Suppl.2): 360–370.

DAHLBERG, M. D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessments. Mar. Fish. Rev. 41: 1–12.

DICKSON, R. R., J. G. POPE, AND M. J. HOLDEN. 1974. Environmental influences on the survival of North Sea cod, p. 69–80. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, NY.

ELLERTSEN, B., P. FOSSUM, P. SOLEMDAL, S. SUNDBY, AND S. TILSETH. 1984. A case study on the distribution of cod larvae and availability of prey organisms in relation to physical processes in Lofoten. *In* E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal [ed.] The propagation of cod *Gadus morhua* L. Flodevigen rapportser 1: 453–477.

1986. Effects of biological and physical factors on survival of Arcto-Norwegian cod and influence on recruitment variability. NAFO SCR Doc. 86/116. Ser. N1243. 25 p.

FLIERL, G. R., AND J. S. WROBLEWSKI. 1985. The possible influence of warm core Gulf stream rings upon shelf water larval fish distribution. Fish. Bull. 83: 313–330.

FORTIER, L., AND W. C. LEGGETT. 1984. Small-scale covariability in the abundance of fish larvae and their prey. Can. J. Fish. Aquat. Sci. 41: 502–512.

FOWLER, G. M., AND S. J. SMITH. 1983. Length changes in silver hake (*Merluccius bilinearis*) larvae: effects of formalin, ethanol, and freezing. Can. J. Fish. Aquat. Sci. 40: 866–870.

FRANK, K. T., F. H. PAGE, AND J. K. MCRUER. 1989. Hydrographic effects on the vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae on the Southwestern Scotian Shelf. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

FRANK, K. T., AND J. K. MCRUER. 1989. Nutritional status of field collected haddock (*Melanogrammus aeglefinus*) larvae from Southwestern Nova Scotia: an assessment based upon morphometric and vertical distribution data. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

GROSSLEIN, M. D., AND R. C. HENNEMUTH. 1973. Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 77–88.

GULLAND, J. A. 1965. Survival of the youngest stages of fish, and its relation to year-class strength. ICNAF Spec. Publ. 6: 363–371.

HANSEN, H., AND E. BUCH. 1986. Prediction of year-class strength of Atlantic cod (*Gadus morhua*) off west Greenland. NAFO Sci. Coun. Studies 10: 7–11.

Harding, D., and J. W. Talbot. 1973. Recent studies on the eggs and larvae of the plaice (*Pleuronectes platessa*) in the southern bight. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 261–269.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 20: 1–228.

Holdway, D. A., and F. W. H. Beamish. 1985. The effect of growth rate, size, and season on oocyte development and maturity of Atlantic cod (*Gadus morhua*). J. Exp. Mar. Biol. Ecol. 85: 3–19.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2: 17–29.

Hurley, P. C. F., and S. E. Campana. 1989. The distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in the waters off Southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Jones, R. 1973. Density dependent regulation of the numbers of cod and haddock. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 156–173.

Koeller, P. A., P. C. F. Hurley, P. Perley, and J. D. Neilson. 1986. Juvenile fish surveys on the Scotian Shelf: implications for year-class size assessments. J. Cons. Int. Explor. Mer 43: 59–76.

Koslow, J. A. 1984. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 41: 1722–1729.

Koslow, J. A., S. Brault, J. Dugas, and F. Page. 1985. Anatomy of an apparent year-class failure: the early life history of the 1983 Browns Bank haddock (*Melanogrammus aeglefinus*). Trans. Am. Fish. Soc. 114: 478–489.

Koslow, J. A., R. I. Perry, P. C. F. Hurley, and R. O. Fournier. 1989. Structure and interannual variability of the plankton and its environment off southwest Nova Scotia in late spring and early summer. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Koslow, J. A., K. R. Thompson, and W. Silvert. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Can. J. Fish. Aquat. Sci. 44: 26–39.

Leggett, W. C., K. T. Frank, and J. E. Carscadden. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 41: 1193–1201.

Lett, P. F., A. C. Kohler, and D. N. Fitzgerald. 1975. Role of stock biomass and temperature in recruitment of southern Gulf of St. Lawrence Atlantic cod, *Gadus morhua*. J. Fish. Res. Board Can. 32: 1613–1627.

Lively, R. R. 1989. Current meter, meteorological, and sea-level observations for Browns Bank, Nova Scotia, April 1983 to May 1985. Can. Tech. Rep. Hydro. Ocean Sci. 113: v + 304 p.

Martin, W. R., and A. C. Kohler. 1965. Variation in recruitment of cod (*Gadus morhua* L.) in southern ICNAF waters, as related to environmental changes. ICNAF Spec. Publ. 6: 833–846.

May, A. W. 1967. Fecundity of Atlantic cod. J. Fish. Res. Board Can. 34: 1531–1551.

Methot, Jr., R. D. 1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull. 81: 741–750.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45: 1657–1670.

Neilson, J. D., E. M. DeBlois, and P. C. F. Hurley. 1988. Stock structure of Scotian Shelf flatfish as inferred from ichthyoplankton survey data and the geographic distribution of mature females. Can. J. Fish. Aquat. Sci. 45: 1674–1685.

O'Boyle, R., K. Frank, and J. Simon. 1989. An evaluation of the population dynamics of 4X haddock 1962–88, with yield projected to 1990. CAFSAC Res. Doc.89/58.

Page, F. H., and K. T. Frank. 1989. Spawning time and egg stage duration in Northwest Atlantic haddock stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Page, F. H., and P. C. Smith. 1989. Particle dispersion in the surface layer off Southwest Nova Scotia: description and evaluation of a model. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Peterman, R. M., and M. J. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science (Wash., DC) 235: 354–356.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45: 8–16.

Powles, P. M. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarius*) in the southwestern Gulf of St. Lawrence. J. Fish. Res. Board Can. 15: 1383–1402.

Randa, K. 1984. Abundance and distribution of 0-group Arcto-Norwegian cod and haddock 1965–1982, p. 189–209. *In* O. R. Godo and S. Tilseth [ed.] Proc. Soviet-Norwegian Symp. on Reproduction and Recruitment of Arctic Cod. Institute of Marine Research. Bergen, Norway.

Rice, J. C., and G. T. Evans. 1986. Non-parametric prediction of recruitment from stock and the relationship of the residuals to water temperature for cod in NAFO Divisions 2J + 3KL and 3M. NAFO SCR Doc. 86/106: 13 p.

Savoy, T. P., and V. A. Crecco. 1988. The timing and significance of density-dependent and density-independent mortality of American shad, *Alosa sapidissima*. Fish. Bull. 86: 467–482.

Shepherd, J. G., and D. H. Cushing. 1981. A mechanism for density-dependent survival of larval fish as the basis of a stock–recruitment relationship. J. Cons. Int. Explor. Mer 139: 160–167.

Shulman, M. J., and J. C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser. 39: 233–242.

Sinclair, M., and T. D. Iles. 1988. Population richness of marine fish species. Aquat. Living Resour. 1: 71–83.

Sissenwine, M. P. 1984. Why do fish populations vary? p. 59–94. *In* R. M. May [ed.] Exploitation of marine communities. Dahlem Konferenzen, New York, NY.

Sissenwine, M. P., E. B. Cohen, and M. D. Grosslein. 1984. Structure of the Georges Bank ecosystem. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 183: 243–254.

Smith, P. C. 1989a. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

1989b. Seasonal and interannual variability off Southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Sundby, S., H. Bjorke, A. V. Soldal, and S. Olsen. 1989. Mortality rates during the early life stages and year class strength of the Arcto-Norwegian cod (*Gadus morhua*), p. 477–500. *In* S. Sundby [ed.] Proc. from workshop on Year Class Variations as Determined from Pre-recruit Investigations. Institute of Marine Research. Bergen, Norway.

Suthers, I. M., and K. T. Frank. 1989. Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in Southwestern Nova Scotia determined with two different gear types. Can. J. Fish. Aquat. Sci. 46: 591–602.

Suthers, I. M., K. T. Frank, and S. E. Campana. 1989. Spatial comparison of recent growth in postlarval cod (*Gadus morhua*) off Southwestern Nova Scotia: inferior growth in a presumed nursery area. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Taggart, C. T., and K. T. Frank. 1989. Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships, p. 1–32. *In* K. Sherman and L. M. Alexander [ed.] Patterns, processes, and yields of large marine ecoystems. AAAS Selected Symposium.

Templeman, W. 1972. Year-class success in some North Atlantic stocks of cod and haddock. ICNAF Spec. Publ. 8: 223–239.

Townsend, D. W., and L. M. Cammen. 1988. Potential importance of the timing of spring plankton blooms to benthic–pelagic coupling and recruitment of juvenile demersal fishes. Biol. Oceanogr. 5: 215–229.

Waiwood, K. G., and M.-I. Buzeta. 1989. The reproductive biology of southwest Nova Scotian Shelf haddock (*Melanogrammus aeglefinus*). Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Zijlstra, J. J., R. Dapper, and J. IJ. Witte. 1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the Western Wadden Sea. Neth. J. Sea Res. 15: 250–272.

Modelling the Initiation of Spring Phytoplankton Blooms: a Synthesis of Physical and Biological Interannual Variability off Southwest Nova Scotia, 1983–85[1]

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Chlorophyll and nitrate data from monthly surveys off southwest Nova Scotia indicate the spring phytoplankton bloom began near the end of March of each year, occurring early (late) in 1984 (1983). The highest chlorophyll biomass (all months) was found in 1985. Using survey data, the Sverdrup hypothesis for the initiation of the bloom was tested by comparing the critical depth, Z_{cr}, for net phytoplankton production to the observed mixed-layer depth, Z_{mix}. Survey median Z_{cr}/Z_{mix} were consistently less than 1 until May, suggesting that observed blooms were initiated by events outside the specific survey periods. Results of a mixed-layer model incorporating surface heating, differential advection and turbulent dissipation by wind and tide showed reasonable agreement with observed mixed depths, and patterns of the mean (modelled) mixed-layer light intensity are significantly correlated with observed chlorophyll biomass. In 1983 and 1984, mean light intensities first exceeded the critical value for a bloom to occur in late March. In 1985, transient periods of stratification in mid-February and early March produced intensities greater than the critical value. These events, together with higher nitrate concentrations and lower zooplankton biomass, appear to be responsible for the high chlorophyll biomass observed in 1985.

Les données sur la chlorophylle et les nitrates recueillies lors de levés mensuels effectués au large du sud-ouest de la Nouvelle-Écosse révèlent que les proliférations printannières de phytoplancton ont commencé vers la fin du mois de mars de chaque année, tôt en 1984 et tard en 1983. La plus forte biomasse de chlorophylle (tous les mois) a été observée en 1985. À l'aide des données des levés, l'hypothèse Sverdrup sur le déclenchement de la prolifération a été mise à l'épreuve en comparant la profondeur critique, Z_{cr}, pour la production nette de phytoplancton, et la profondeur observée de la couche mixte, Z_{mix}. La médiane Z_{cr}/Z_{mix} des levés était constamment inférieure à 1 jusqu'au mois de mai, ce qui laisse croire que les proliférations observées étaient déclenchées par des événements indépendants des périodes de levé. Les résultats d'un modèle de couche mixte incorporant le réchauffement en surface, l'advection différentielle et la dissipation turbulente par le vent et les marées révèlent une concordance raisonnable avec les profondeurs mixtes observées; les configurations de l'intensité lumineuse moyenne de la couche mixte (modélisée) sont correliées de façon significative à la biomasse observée de chlorophylle. En 1983 et en 1984, les intensités lumineuses moyennes ont d'abord dépassé la valeur critique pour une prolifération qui a eu lieu à la fin mars. En 1985, des périodes transitoires de stratification à la mi-février et au début mars ont produit des intensités supérieures à la valeur critique. Ces événements, de concert avec les concentrations élevées de nitrate et la faible biomasse de zooplancton, semblent être à l'origine de la forte biomasse de chlorophylle observée en 1985.

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The match–mismatch hypothesis has been an important concept of fisheries ecology since first suggested for herring by Iles (1964) and formulated by Cushing (1967). It proposes that recruitment success of marine fish stocks is improved when the seasonal spawning cycle of the stock coincides with peaks in the seasonal production cycle of phytoplankton and subsequently zooplankton. Variation in spawning times is controlled, in part, by light and temperature (Bye 1984), which are also two of the critical parameters in the plankton production cycle. Therefore, interannual variability in certain physical properties can influence both components of the match–mismatch hypothesis.

The inclusion of similar parameters in the possible control of both plankton production and spawning times was noted for gadid stocks in the Northwest Atlantic by Templeman (1972). He suggested that, while natural selection will have matched average spawning times with the average timing of spring blooms, the matching might not occur in any one year or group of years. Such variability could lead to recruitment failure, assuming the early larval phase is considered a critical period for year-class formation. The identification of factors influencing the distribution and survival of the larval stages of haddock (*Melanogrammus aeglefinus*) (and Atlantic cod (*Gadus morhua*)) off Southwest Nova Scotia has been a major focus of the Fisheries Ecology Program (FEP) (e.g. Hurley and Campana 1989; Campana et al. 1989). However, while analyses have been conducted of the potential variability in spawning times of haddock in southwest Nova Scotia (Waiwood and Buzeta 1989; Page and Frank 1989), no analysis has examined the variation in timing of the spring phytoplankton bloom in the study area, in particular during the FEP period 1983–85.

The principal objective of this paper is to determine interannual differences in timing and magnitude of the spring phytoplankton bloom between 1983–85. We examine parameters relevant to the Sverdrup (1953) critical depth–mixed depth hypothesis for the initiation of blooms on a survey-by-survey basis to identify factors contributing to the variability. Based on this hypothesis, we develop a model for the mixed-layer depth in continental shelf areas which combines the buoyancy effects of surface heating and freshwater flux and the turbulent dissipation due to the wind and tide. Mean light intensities through these mixed layers are calculated for each day, and compared with a critical value for the development of phytoplankton blooms.

Modelling the initiation of the spring phytoplankton bloom serves as a synthesis of the interannual variation of several physical and biological properties pertinent to the distribution and survival of larval haddock. These include solar radiation and its impact on surface heating and phytoplankton growth; surface wind stress and its influence on turbulent mixing and advection; changes in freshwater flux induced by precipitation, evaporation, or advection; nutrient concentrations; and phytoplankton and zooplankton biomass. We conclude with a discussion of the seasonal processes affecting phytoplankton production off southwest Nova Scotia, combining results of studies conducted during late spring (Koslow et al. 1989), summer (Fournier et al. 1984b), and fall (Fournier et al. 1984a).

Methods

The Fisheries Ecology Program larval sampling grid consisted of 95 stations (Hurley and Campana 1989); however, a reduced number of stations (41) was used in this study for the measurement and analysis of chlorophyll biomass and nutrient concentrations. These 41 stations were selected to include the inshore southwest Nova Scotia region, and across Browns Bank to the northern edge of the Northeast Channel (Fig. 1a). Surveys were conducted from February to May 1983 to 1985 (Fig. 1b). The number of stations occupied on each survey and the dates these stations were sampled are indicated in Table 1. Lines 15 and 16 (Fig. 1a) were added to the survey grid in 1984 and 1985 to provide better resolution over the cap of Browns Bank.

Spatial analyses of physical and biological properties on each survey were summarized into five areas, representing different depth and tidal mixing regimes (Fig. 2). These were a shallow, inshore, tidally well-mixed region (Area 1); a tidally-induced summer-frontal region along the 60–100 m isobaths of the inshore region (Area 2); a deep (>100 m), summer-stratified region surrounding Browns Bank (Area 3); a region of varying bathymetry about the edge of Browns Bank (Area 4); and Browns Bank itself (Area 5). The mixed, frontal, and stratified regions were defined as in Koslow et al. (1989) from the stratification parameter of Garrett et al. (1978) and Loder and Greenberg (1986).

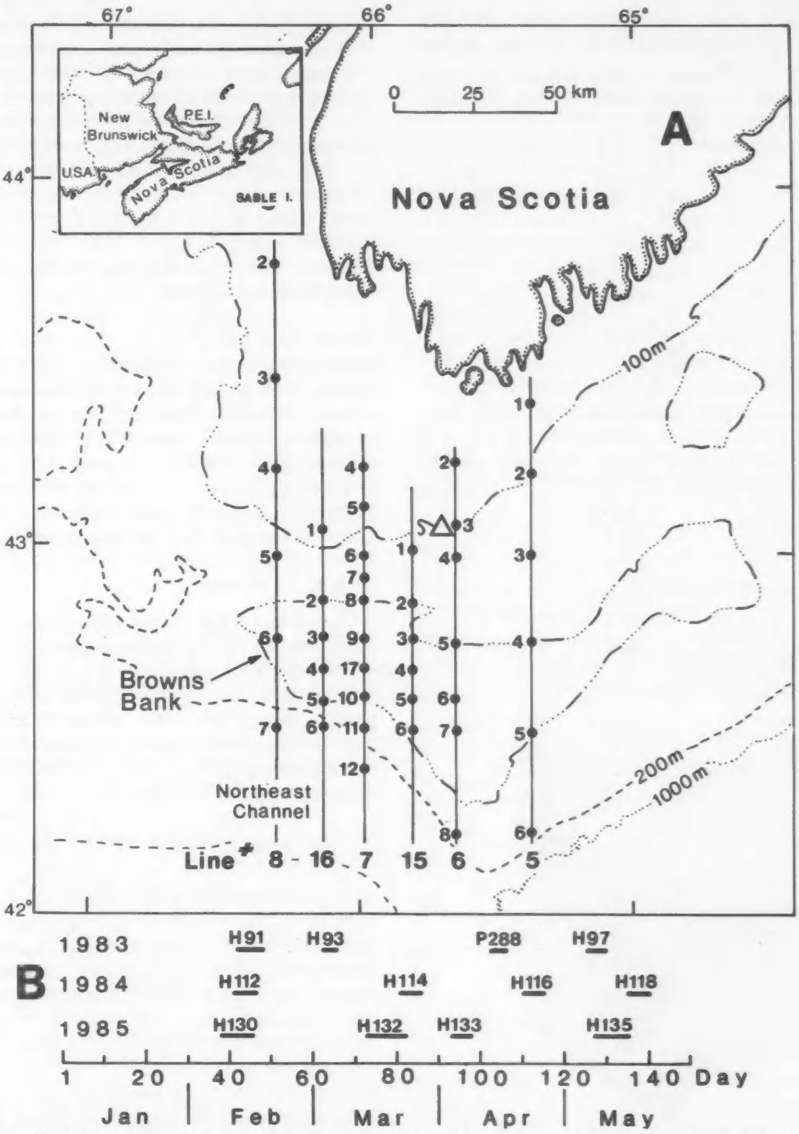
Measured Parameters

Temperature and salinity were sampled to within 10 m of the bottom at each station using a Guildline conductivity-temperature-depth (CTD) instrument. In 1983, due to malfunctioning equipment, data were recorded only from the depths 1, 10, 20, 30, 40, 50, 75, 100, 125, 150, 175, 200 m and 10 m above bottom. In 1984 and 1985, CTD data were recorded continuously to at least 10 m above bottom. Data for each set were summarized as mean integrated upper layer (1–50 m) temperatures and salinities, for comparison with other upper layer bulk properties. The 50-m level approximated the measured mixed-layer depth on most cruises in late spring, and represented the maximum depth sampled for phytoplankton pigments.

Temperature and salinity were measured continuously during 1983, 1984, and 1985 from a mooring (C2) located on the 110-m isobath in the frontal region (Fig. 1a). Current meters, recording current speed and direction, temperature, and salinity, were located near the surface (15 m), at mid-depth, and near-bottom (10 m above). Instrument accuracies and performance records are discussed by Smith (1989a). These data are summarized as monthly means for February to June, 1983–85; annual cycles and interannual variability over the period 1978–85 are also discussed by Smith (1989b).

Chlorophyll *a* (as an index of phytoplankton biomass), nitrate, and zooplankton displacement volume were also measured. Water samples for chlorophyll and nitrate analyses were collected at each station using a rosette sampler. Nutrients were analysed from 1, 10, 20, 30, 40, 50, 75, 100, 125, 150 m and 10 m above bottom, while chlorophyll *a* was determined from the 50-m and shallower depths. Samples were filtered and frozen onboard, and analysed ashore following standard techniques (Parsons et al. 1984a), using the fluorometric procedure for chlorophyll *a* and the colorimetric auto analyser procedure for nitrate. In order to represent the temporal and spatial pattern of chlorophyll, these data were integrated to 50-m and expressed as weight per unit surface area. Individual nitrate measurements were similarly converted to nitrate per unit surface area.

Zooplankton were collected from each station using a paired 61-cm diameter bongo sampler, towed obliquely from a depth of 5 m above bottom (or a maximum of 200 m) to the surface.



67°
66°
65°
44°
43°
42°
New Brunswick
P.E.I.
U.S.A.
Nova Scotia
SABLE I.
0 25 50 km
A
Nova Scotia
100m
200m
1000m
Browns Bank
Northeast Channel
Line# 8 - 16 - 7 15 6 5
B
1983 H91 H93 P288 H97
1984 H112 H114 H116 H118
1985 H130 H132 H133 H135
1 20 40 60 80 100 120 140 Day
Jan Feb Mar Apr May

FIG. 1. (A) Locations of lines and stations sampled in this study, consisting of a reduced Fisheries Ecology Program sampling grid. Numerals indicate station numbers. The triangle identifies the location of mooring C2; the inset identifies the location of Sable Island, where meteorological parameters were measured. (B) A comparison of sampling times for this station grid, in 1983, 1984, and 1985, with cruise numbers indicated.

Net mesh size was 333 μm, and volumes filtered were determined using General Oceanics flowmeters mounted in the mouth of each net. Zooplankton biomass was analysed as displacement volume, then identified to broad taxonomic categories, e.g. copepods, ctenophores, etc., and grossly enumerated as $\log_{10}$ abundance indices (e.g. 1 (1–9 individuals), 2 (10–99), 3 (100–999), 4 (>999)). No plankton were removed from the samples before displacement volumes were measured. Since this could cause an overestimation of plankton volumes for samples with abundant ctenophores (considering their large volume), a *t*-test was conducted between displacement volumes in which the ctenophore abundance index was <3 and ≥ 3, for each survey. Displacement volumes from stations with ctenophore abundances of 3 or 4 were excluded from further analyses if the test indicated a significant difference ($p<0.05$). This excluded 5, 3, 2, 12, 3, and 7 stations from surveys H091, H093, P288, H097, H116, and H118, respectively.

Meteorological data during the study period January to May 1983 to 1985 were obtained from the Atmospheric Environment Service as regularly recorded at their station on Sable Island (Fig. 1a, inset). Parameters observed included wind speed, air temperature, and dew point temperature, all calculated as daily

TABLE 1. Cruise numbers, start and end sampling dates, and number of stations occupied of the reduced Fisheries Ecology Program sampling grid used in this study.

Year	Cruise number	Sampling dates	No. of stations
1983	H091	11–17 Feb.	27
	H093	14–16 Mar.	22
	P288	13–16 Apr.	15
	H097	6–10 May	27
1984	H112	10–16 Feb.	27
	H114	22–27 Mar.	41
	H116	19–25 Apr.	39
	H118	16–21 May	41
1985	H130	6–15 Feb.	41
	H132	14–24 Mar.	34
	H133	3–8 Apr.	40
	H135	7–12 May	40

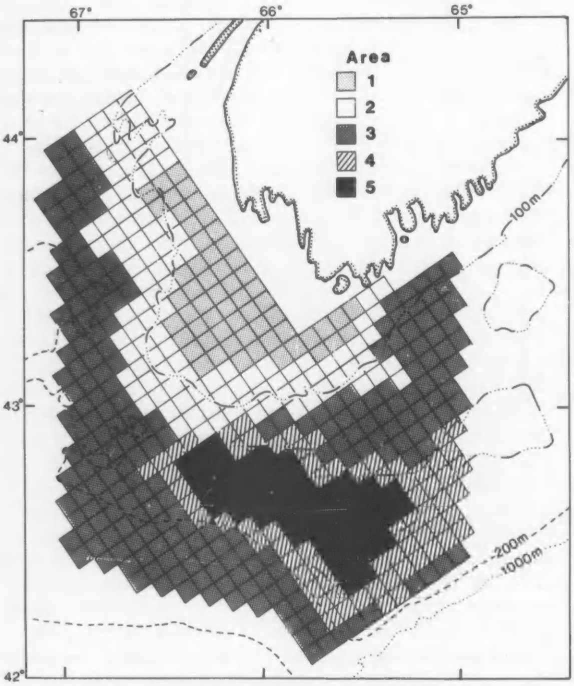


FIG. 2. Reduced segment of Greenberg's (1983) tidal model grid for southwest Nova Scotia, that was used in this study for the mixed-layer model. The shading identifies the areas used to define the inshore region (Area 1), the frontal region (Area 2), the deep stratified region (Area 3), the region around Browns Bank (Area 4), and the Browns Bank region (Area 5).

means from hourly observations, and total daily solar radiation. Daily mean wind speeds were converted to wind stress (τ), using $\tau = \rho_a k_a \bar{W}^2$ (Pond and Pickard 1983; symbols defined in Table 2). In this analysis, Sable Island data were chosen to measure atmospheric forcing at the sea surface because they are representative of open ocean conditions and relatively free from terrestrial influences. Wright et al. (1986) found Sable Island winds to be a reasonable proxy for low-frequency atmospheric forcing over the Gulf of Maine, while Smith (1987) found monthly mean vector wind stress at Sable Island to be four times that measured at Halifax but consistent with buoy measurements just 30 km offshore. Due to the large scales, atmospheric forcing is generally coherent over the Scotian Shelf, with small lags of <12 h from west to east, consistent with the movement of major weather systems (e.g. Smith and Petrie 1982).

Total daily solar radiation values were converted from megajoules per square metre per day to Watts per square metre using 1 $\mathrm{MJ \cdot m^{-2} \cdot d^{-1} = 11.5\ W \cdot m^{-2}}$. Missing daily solar radiation values (2,1, and 12 in 1983, 1984, and 1985) were replaced with clear sky theoretical maximum values using (Townsend and Spinrad 1986)

$$(1)\quad I_o = a + b \sin \omega t$$

with the following coefficients appropriate for the Gulf of Maine: a = the minimum daily irradiance, occurring on the winter solstice (72.2 $\mathrm{W \cdot m^{-2}}$), b = the difference in daily irradiance between winter and summer solstices (264.7 $\mathrm{W \cdot m^{-2}}$), $\omega = \pi/365\ \mathrm{d^{-1}}$, and $t=0$ corresponding to 21 December. Total daily solar radiation and mean daily wind stress are also summarized as monthly means over the study period to compare their interannual variability (Table 4).

Derived Parameters

The critical depth–mixed depth model (Sverdrup 1953) proposes that the spring phytoplankton bloom will occur (given sufficient nutrients) once the critical depth, defined as the depth at which total photosynthesis equals total phytoplankton respiration through the water column, exceeds the depth of the upper mixed layer. In practice, the critical depth is calculated by determining the depth at which the vertically-integrated mean light intensity equals some critical value:

$$(2)\quad \bar{I}_{Z_{cr}} = \frac{I_0}{2\,\kappa\, Z_{cr}}\left(1 - e^{-\kappa Z_{cr}}\right)$$

with I_o the irradiance just below the sea surface, κ the average light attenuation coefficient for the given station, and Z_{cr} the daily critical depth to be calculated (Parsons et al. 1984b). This equation was solved for Z_{cr} using the Newton-Raphson iterative method (e.g. Seber 1973) by setting $\bar{I}_{Z_{cr}} = 19.25\ \mathrm{W \cdot m^{-2}}$. This value of $\bar{I}_{Z_{cr}}$ has been found to be the minimum depth-averaged vertically-integrated light intensity needed to initiate a phytoplankton bloom (Riley 1957; Gieskes and Kraay 1975; Pingree et al. 1976; Townsend and Spinrad 1986).

In order to incorporate the temporal averaging nature of phytoplankton growth, in which growth rates integrate the light history over a 3–4 d period (Platt and Jassby 1976; Savidge 1988), the daily solar radiation values were smoothed with a 4-d weighted average. The weights used were 0.1, 0.2, 0.3, 0.4 with the largest weight applied to the solar radiation for the day the station was sampled, and successively smaller weights applied to the days prior to sampling. Attenuation coefficients were calculated from Secchi depth (Z_s) measurements at each station by $\kappa = 1.7/Z_s$ (Parsons et al. 1984b). To include as many stations as possible in the analysis, stations that were sampled at night were assigned the median daytime Secchi depth values for the appropriate survey and area, with area defined as in Fig. 2.

The principal consideration of the critical depth–mixed depth model is whether phytoplankton are likely to be mixed deeper than the critical depth. To determine the extent of mixing, we calculated the potential energy anomaly ($\bar{\phi}_{Z_{cr}}$ $\mathrm{J \cdot m^{-3}}$) from the surface to the critical depth. This quantity represents the amount of mechanical energy (per unit volume) required to completely homogenize the surface layer to a depth, Z_{cr} (Simpson 1981; Richardson et al. 1985). Larger values represent more strongly stratified waters within the depth range of integration. The potential energy anomaly was calculated from temperature and salinity profiles at each station as (Simpson 1981),

$$(3)\quad \bar{\phi} = \frac{1}{h}\int_{-h}^{0} (\bar{\rho} - \rho)\, g_z\, d_z, \quad \bar{\rho} = \frac{1}{h}\int_{-h}^{0} \rho\, d_z;$$

with h = the layer depth; ρ and $\bar{\rho}$ the density and mean density of the layer, respectively; g the acceleration due to gravity (9.8 $m \cdot s^{-2}$); and Z the depth (positive upwards).

To determine the depth of the surface mixed layer, the stations were first classified according to their potential energy anomalies calculated over the full water column (i.e. $h = Z_{max}$, where Z_{max} is located at most 10 m above bottom). This provided an objective measure of the extent of mixing throughout the entire water column. For those stations that were identified as vertically homogeneous ($\phi_{Z_{max}} \leq 5\ J \cdot m^{-3}$), the depth of the bottom was assigned as the mixed layer depth. Otherwise, the mid-point of the maximum gradient in density, $\max(\Delta\sigma_t/\Delta Z)$, was defined as the depth of the surface mixed layer.

A Model for the Initiation of the Spring Bloom

Calculation of the critical depth, and the mean light intensity to the critical depth, are relatively straightforward (e.g. equation (2)). Modelling the mixed-layer depth is more difficult, involving energy balances between vertical and horizontal fluxes of buoyancy (including differential advection; Van Aken 1986), the production of turbulence at the sea surface by the wind and, in shallow shelf seas, the production of turbulence by tidal currents flowing over the sea bottom. In this section, we develop a model for the mixed-layer depth to be used in equation (2) to calculate the mean light intensity throughout the (modelled) mixed-layer. A bloom is assumed to occur when the mean light intensity becomes greater than the critical value of 19.25 $W \cdot m^{-2}$ (see previous section).

The mixed-layer model is based on considerations of tidal fronts, separating well-mixed from stratified water masses. The location of a tidal front is determined by a balance between stratifying (buoyancy supplied by heat and freshwater) and mixing (wind and tide-induced turbulence) processes. In the one-dimensional case, the rate of increase of the potential energy anomaly per unit surface area is augmented by surface heating and diminished by dissipation due to tides (D_t) and wind (D_w) (Simpson and Hunter 1974; Bowers and Simpson 1987):

$$h\frac{d\bar{\phi}}{dt} = \frac{g\alpha Q h}{2\, c_p} - (\epsilon_t'\, D_t + \epsilon_w\, \gamma\, D_w)$$

(definitions of all symbols used in this model are given in Table 2). Vertical mixing by the tides is expressed as a fixed fraction of the tidal dissipation, $\epsilon_t'\, D_t$, where $D_t = \rho\, C_D \langle (U^2 + V^2) \rangle^{3/2}$ and ϵ_t' is the reduced tidal mixing "efficiency" in the presence of wind mixing (Loder and Greenberg 1986). The turbulent

TABLE 2. Definition of symbols used in the development of the surface mixed-layer model.

Symbol	Definition	Approximate value	Reference
g	Acceleration due to gravity	$9.8\ m \cdot s^{-2}$	
α	Coefficient of expansion of sea water	$1.6 \times 10^{-4}\ °C^{-1}$	Dorrestein 1979
Q	Surface heat flux		
c_p	Specific heat of sea water	$4 \times 10^3\ J \cdot kg^{-1} \cdot °C^{-1}$	Loder and Greenberg 1986
C_D	Bottom drag coefficient	0.0027	Loder and Greenberg 1986
ρ	Density of sea water		
ρ_o	Reference density of sea water	$1025\ kg \cdot m^{-3}$	
U,V	M_2 model current components		Greenberg 1983
U_*	Bottom friction velocity ($m \cdot s^{-1}$)		
f	Coriolis parameter	$10^{-4} s^{-1}$	
ϵ_t'	Reduced tidal mixing "efficiency"	1.5×10^{-3}	Loder and Greenberg 1986
ϵ_w	Wind mixing "efficiency"	$\epsilon_w\gamma = 0.9 \times 10^{-3}$	Loder and Greenberg 1986
( )	( )		
γ	Ratio of wind-induced surface layer speed to wind speed		
k_a	Air–water drag coefficient	1.4×10^{-3}	Pond and Pickard 1982
ρ_a	Air density	$1.2\ kg \cdot m^{-3}$	Loder and Greenberg 1986
h	Mixed layer depth(m)		
$\bar{W}$	Daily mean wind speed at 10 m ($m \cdot s^{-1}$)		
β	Coefficient of haline contraction	$7 \times 10^{-4}\ (‰)^{-1}$	Dorrestein 1979
S	Salinity (‰)		
H	Depth of bottom (m)		
B	Surface buoyancy flux ($kg \cdot m^{-2} \cdot s^{-1}$)		
Z	Depth (m)		
K	Vertical diffusivity	$20\text{–}200 \times 10^{-4} m^{-2} s^{-1}$	Loder et al. 1988 and Smith 1989b.
$\langle . \rangle$	Average over a tidal period		
τ	Surface wind stress (pa)		
ΔZ	Depth interval between midwater and near-surface instruments at C2	35 m	
$\frac{\partial \Delta S}{\partial t}$	Rate of change of vertical (50–15 m) salinity contrast at C2		
k	Thermal exchange coefficient ($W \cdot m^{-2} \cdot s^{-1}$)		
κ	Average light attenuation coefficient (m^{-1})		

mixing due to the wind is $\epsilon_w \gamma k_a \rho_a \bar{W}^3 = \epsilon_w \gamma D_w$, with ϵ_w the wind mixing "efficiency" and γ the ratio of the wind-induced surface layer speed to the wind speed. Vertically well-mixed conditions are predicted for $h\, d\bar{\phi}/dt < 0$, where dissipation exceeds the buoyancy flux, and stratified conditions for $h\, d\bar{\phi}/dt > 0$, where dissipation is less than the surface buoyancy flux. Therefore, a frontal region will occur where the rate of increase of potential energy due to surface buoyancy fluxes is balanced by the rate of decrease of potential energy by wind and tidal dissipation, i.e. (Bowers and Simpson 1987)

$$(4) \quad \epsilon_t' D_t + \epsilon_w \gamma D_w = \frac{g\alpha Q h}{2\, c_p},$$

or

$$\frac{\epsilon_t' D_t + \epsilon_w \gamma D_w}{g\alpha Q / 2\, c_p} = h.$$

In the absence of tides, equation (4) has the form of the Monin-Obukhov length, representing the depth at which the magnitudes of the energy input from the Reynolds stresses and the buoyancy flux terms become comparable (Phillips 1966). This length scale is relevant for cases of strong surface heating (Niiler and Kraus 1977) in which the wind is just sufficient to mix the layer to a depth of,

$$(5) \quad h_w = \frac{\epsilon_w \gamma D_w}{g\alpha Q / 2\, c_p}$$

without causing significant entrainment at the base of the mixed layer. This is the appropriate formulation for shoaling of the mixed layer which occurs during spring.

However, the region off southwest Nova Scotia cannot be considered horizontally uniform (as demanded by the one-dimensional constraint) since it is strongly dominated by horizontal advection of low salinity water masses, particularly during winter (Smith 1989b). In addition, freshwater inputs may have an important effect on the surface fluxes of buoyancy, and should not be neglected in development of the model. The principal sources of freshwater fluxes are the excess of precipitation (P) over evaporation (E) at the surface, and differential advection of the salt-stratified density field (Smith (1989b) has demonstrated that the seasonal cycle in salinity off Southwest Nova Scotia is determined primarily by horizontal advection). Assuming (1) that density is controlled by salinity, and (2) that density changes near the top and bottom of the water column are determined by horizontal advection in the alongshore (y) direction, the work of Van Aken (1986) may be used to derive the equation for the rate of change of potential energy including surface heat and freshwater fluxes, horizontal advection, and wind and tidal dissipation (see Appendix I for derivation),

$$(6) \quad h\,\frac{d\bar{\phi}}{dt} = -\frac{1}{2}\,\rho_0\, h\, B_0 + \frac{g\, h^3}{3\,\Delta Z}\,\rho_0\, \beta\, \frac{\partial\, \Delta S}{\partial t} - (\epsilon_t' D_t + \epsilon_w \gamma D_w)$$

where $B_0 = -\dfrac{g}{\rho_0}\left(\dfrac{\alpha Q}{c_p} + \beta\, S\, (P-E)\right)$ (Dorrestein 1979),

and ΔS is the vertical contrast in salinity over the depth interval ΔZ. Noting that monthly average excess of precipitation over evaporation is about +10 cm and that a typical daily vertical (50–15 m) contrast in salinity at mooring C2 is about 0.05 ‰, the surface fluxes of freshwater due to precipitation are a relatively small (5–10%) proportion of that due to horizontal advection and are therefore neglected in this model. Equation (6) then reduces to

$$(7) \quad h\,\frac{d\bar{\phi}}{dt} = \underset{\text{A}}{\frac{g\alpha Q h}{2\, c_p}} + \underset{\text{B}}{\frac{g\, h^3}{3\,\Delta Z}\,\rho_0\, \beta\, \frac{\partial\, \Delta S}{\partial t}} - \underset{\text{C}}{(\epsilon_t' D_t + \epsilon_w \gamma D_w)}$$

To determine the depth at which the processes increasing the potential energy (A, B) balance the processes decreasing the potential energy (C), ($h\, d\bar{\phi}/dt$) is set equal to 0 and the resulting condition is solved for h. The solutions to this cubic equation for positive values of h are detailed in Appendix II. Note, however, that equation (7) does not take account of the physical separation of the different sources of turbulent diffusion, i.e. the wind at the surface and the tide at the bottom, and in particular, assumes that bottom-generated turbulence is not significantly reduced in the region $-h \leq Z \leq 0$. It therefore overemphasizes the work of tidal dissipation against the near-surface buoyancy fluxes. In order to include the effect of these different source regions in the model, the thickness of the bottom Ekman layer was estimated as (Loder and Greenberg 1986):

$$(8) \quad h_E = \frac{0.2\, U_*}{f}, \quad U_* = (C_D \langle U^2 + V^2 \rangle)^{1/2}$$

where f is the Coriolis parameter and U_* is the average bottom friction velocity. If the total depth of the water column exceeds both the frontal mixed depth, h, and the Ekman depth, h_E, then local tidal dissipation should not make a significant contribution to the work against gravity near the surface. In those cases, the effect of tides was excluded from equation (7) so that the mixed-layer depth was determined solely by wind dissipation, i.e. the equivalent of using equation (5) but including differential advection.

Input values for the variables defined in the model were taken from the following sources. Tidal dissipation (D_t) values were obtained from the 2-D tidal model of the Gulf of Maine by Greenberg (1983), for the grid squares within the region of interest (Fig. 2). Surface buoyancy fluxes and turbulent dissipation rates were calculated for each of these grid squares and the solutions were averaged over the defined areas. Wind dissipation (D_w) was calculated as $\rho_a k_a \bar{W}^3$ (Pond and Pickard 1983), with $\bar{W}$ the mean daily wind speed as measured on Sable Island during the period of interest. The equations used to calculate the surface heat flux (Q) are from James (1977) and Simpson and Bowers (1984) (Appendix III), using daily mean values of solar radiation, air temperature, and dew point temperature measured on Sable Island. Vertical salinity contrasts (ΔS) were calculated as the difference between the mid-depth and near-surface (50–15 m) instruments at mooring C2. These data are highly variable on wind-driven time scales (periods of 2–10 d; Smith 1989a), so a 10-d moving filter was applied before calculating the daily differences in the vertical salinity contrast ($\partial \Delta S/\partial t$). On this time scale, the neglect of vertical diffusion in the derivation of the differential advection term may be questioned since vertical diffusion time scales are similar (see below). The attenuation coefficient (κ) in the mixed layer light intensity (equation (2)) was set at 0.12 for days prior to 16 March (Day of Year 75), and 0.13 for days after this date, to take account of the increased attenuation of light due to higher phytoplankton biomass in spring.

The daily layer depths, h, computed from equation (7) (with or without tides), were substituted for Z_{cr} in equation (2) to obtain an estimate of the mean daily light intensity within the

TABLE 3. Summary statistics for parameters measured on each survey. Values are survey means (x) and standard errors (SE) (n >14 for all parameters). Z_{cr} = critical depth; Z_{mix} = mixed-layer depth; Z_{max} = bottom depth.

Month	Year	Cruise number	Mean temp. to 50 m (°C)		Mean salinity to 50 m (‰)		Chlorophyll (mg·m^{-2})		Nitrate (mM·m^{-2}) to Z_{max}		Zooplankton displacement volume (mL·m^{-2})		Critical depth (m)		Mixed depth (m)		Potential energy anomaly (J·m^{-3})		Median Z_{cr}:Z_{mix} ratio
			x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	
Feb.	1983	H091	4.14	0.17	31.84	0.09	7.1	0.6	665	71	11.5	1.8	11.4	1.2	81.8	8.1	0.1	0.1	0.15
	1984	H112	3.65	0.20	32.00	0.09	9.8	0.6	616	77	9.1	1.1	14.2	1.5	60.9	7.4	1.5	0.4	0.23
	1985	H130	2.43	0.13	31.75	0.04	11.6	0.5	665	52	9.9	1.0	12.5	0.7	36.8	4.9	1.7	0.5	0.38
Mar.	1983	H093	3.08	0.23	31.72	0.11	19.6	1.6	562	93	9.1	1.1	19.7	0.9	64.9	5.7	0.9	0.3	0.31
	1984	H114	2.66	0.20	31.78	0.16	50.4	5.7	709	84	9.7	1.7	29.1	2.6	78.2	9.8	2.7	0.9	0.67
	1985	H132	2.77	0.17	31.88	0.05	84.1	7.3	810	74	9.2	1.0	33.9	1.9	76.9	7.7	1.6	0.3	0.44
Apr.	1983	P288	3.67	0.25	31.95	0.10	46.8	10.6	343	66	33.3	4.0	21.8	0.7	71.2	5.7	2.1	1.4	0.40
	1984	H116	2.87	0.15	31.86	0.07	39.9	2.9	280	63	25.5	3.1	30.8	1.0	56.1	4.3	2.5	0.6	0.56
	1985	H133	2.50	0.18	31.82	0.07	140.0	15.1	688	75	13.7	1.5	26.2	1.0	56.7	5.7	4.7	1.2	0.42
May	1983	H097	4.84	0.13	31.88	0.07	17.2	2.2	444	68	30.8	6.0	57.6	3.8	43.1	6.0	30.6	5.1	1.54
	1984	H118	5.15	0.14	32.19	0.07	15.4	1.1	529	75	30.0	2.7	36.8	1.1	51.7	6.4	11.4	1.4	0.88
	1985	H135	3.90	0.13	31.99	0.08	51.3	5.9	414	38	56.0	4.8	53.2	2.3	44.1	5.2	22.7	3.6	1.97

mixed layer. If the calculated layer depth exceeded the local depth, the latter was used in place of h. The choice of a daily sampling interval for the calculations was convenient, but the results do not necessarily represent equilibrium conditions in the mixed layer. The balance condition for equation (7) implies that a steady state exists between the forces tending to increase and decrease the potential energy of the water column. The time required to establish equilibrium with surface forcing in a typical layer depth of 50 m could be determined from the vertical diffusivity, K, but estimates for this region cover a wide range ($20\leq K\leq 200 \times 10^{-4}$ m$^2\cdot$s^{-1}; Loder et al. 1988; Smith 1989b), corresponding to diffusive time scales (Z^2/K) of 1.5 to 15 d. In view of this, we have chosen to smooth the daily mean mixed-layer light intensities with a 3-d moving average. This time scale is similar to a scale of 3–4 d for phytoplankton production suggested by Platt and Jassby (1976) and Savidge (1988).

Results

Physical Conditions

The mean bottom depth for each of the areas identified in Fig. 2 is an important parameter since it controls the influence of tidal mixing and the presence of a deep reservoir of nutrients. The mean depths for each area as measured at the stations identified in Fig. 1a are

	Area 1	2	3	4	5
Mean (m)	60	108	160	125	87
SE (m)	1	3	5	3	1
n	66	74	109	128	149

Survey mean hydrographic properties are presented in Table 3, calculated as mean depth-integrated values over the upper 50 m. Temperatures through the upper 50 m reached a minimum during March in 1983 and 1984, while in 1985 they varied less than 0.25°C from February to April. Temperatures in May in all years were warmer than on earlier surveys, with the largest increase in survey-mean temperature (2.3°C) occurring in 1984. The warmest year over the period February to May was 1983 (mean 3.93°C), and the coolest year (mean 2.90°C) was 1985. These patterns are corroborated by the monthly means from near-surface and mid-depth instruments moored at location C2 (Table 4). Specific differences in magnitude indicate the variability within the study region, reflecting the broader spatial coverage of the surveys compared with the single mooring site where the temporal resolution was superior.

In general, surveys with warmer mean temperatures (integrated to 50 m) also had higher mean salinities (Table 3). This is consistent with the strong correlation (r^2>80%) of temperature and salinity, at least during February, March, and April. In contrast to temperature, no year emerged as consistently the freshest in all months, based on survey mean 50-m integrated values. Monthly mean near-surface salinities for C2, however (Table 4), indicate 1983 was the freshest year from February to April. This is consistent with Smith (1989b), who noted a large negative salinity anomaly at C2 during 1983. The discrepancy with mean survey data can be explained by the integration to 50 m and the broader area covered during the surveys. Nonetheless, the interannual trends are comparable between survey and monthly C2 statistics.

Biological Conditions

Survey summary statistics for nitrate, chlorophyll a, and zooplankton displacement volume are presented in Table 3. In addition, survey means and standard errors for chlorophyll $a\cdot$m^{-2} integrated to 50 m are shown in Fig. 3 for comparison between years, which also illustrates the variation in survey timing. The major feature is the much larger chlorophyll biomass in 1985 compared with the previous two years. Calculation of mean chlorophyll $\cdot$ m^{-2} (to 50 m) by area (Fig. 4) indicates that while 1985 had high chlorophyll biomass in all areas, it was the offshore regions (areas 3, 4, 5) which had the highest concentrations. The inshore region (Area 1) consistently had lower chlorophyll biomass than offshore regions, except for the March 1985 survey (H132, Fig. 4) during which only two stations were sampled in that area. Due to the variability in timing of the surveys, only in March 1984 did the peak chlorophyll biomass appear to occur earlier in the offshore regions (March)

TABLE 4. Summary statistics for parameters measured continuously during each month. Values are means (*x*) and standard errors (SE).

						C2 temperature (°C)						C2 salinity (‰)					
		Wind stress ($\times 10^{-2}$Pa)		Solar radiation ($W \cdot m^{-2}$)		Near-surface (15 m)		Mid-depth (50 m)		Near-bottom (100 m)		Near-surface (15 m)		Mid-depth (50 m)		Near-bottom (100 m)	
Month	Year	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE
Feb.	1983	16.9	2.6	74.90	4.72	3.72	0.05	4.00	0.06	4.73	0.07	31.61	0.01	31.54	0.01	31.92	0.02
	1984	10.7	1.1	71.23	6.47	3.47	0.07	4.20	0.08	4.90	0.07	32.04	0.03	32.28	0.03	32.23	0.03
	1985	14.6	1.7	107.36	10.68	1.92	0.06	2.96	0.07	4.30	0.08	31.78	0.01	32.04	0.02	32.44	0.02
Mar.	1983	14.1	2.2	119.63	9.76	2.26	0.03	2.54	0.03	3.24	0.03	31.49	0.01	31.44	0.01	31.72	0.01
	1984	13.9	1.8	127.43	11.15	2.32	0.06	2.93	0.01	3.70	0.01	31.81	0.02	31.92	0.04	31.83	0.05
	1985	15.6	1.9	162.87	13.76	2.41	0.04	3.09	0.02	4.17	0.03	31.98	0.01	32.29	0.01	32.58	0.01
Apr.	1983	7.4	0.9	166.54	12.39	2.65	0.08	2.57	0.09	3.08	0.09	31.51	0.02	31.81	0.03	32.09	0.03
	1984	13.1	1.7	138.44	12.62	1.92	0.02	1.99	0.02	2.54	0.03	31.65	0.07	31.68	0.08	31.55	0.01
	1985	10.6	1.5	202.56	16.86	2.74	0.08	3.21	0.07	4.09	0.07	31.96	0.02	32.41	0.02	32.61	0.03
May	1983	5.1	0.7	200.27	15.37	5.01	0.04	4.32	0.06	4.58	0.08	31.75	0.03	32.34	0.03	32.60	0.03
	1984	8.1	0.9	211.39	16.63	3.94	0.01	3.82	0.01	4.10	0.01	31.95	0.04	32.15	0.04	31.93	0.05
	1985	8.2	1.1	247.52	17.32	3.38	0.04	3.15	0.03	3.67	0.02	31.73	0.01	32.28	0.11	32.44	0.01

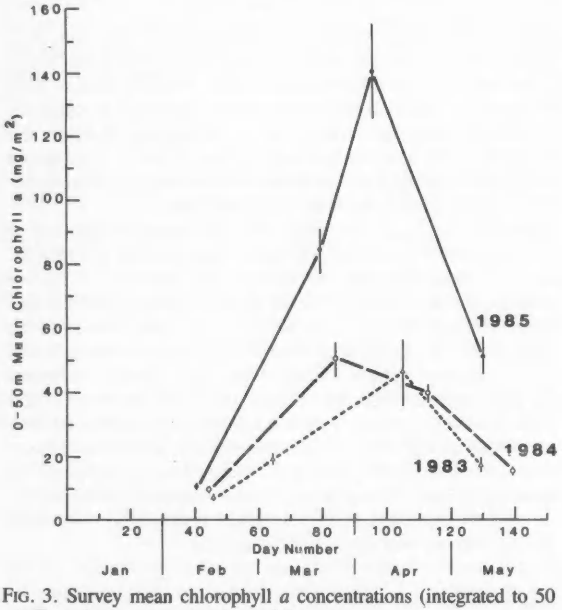


FIG. 3. Survey mean chlorophyll *a* concentrations (integrated to 50 m). Error bars represent ± 1 SE of the mean.

than inshore (Area 1; April). In all years, chlorophyll biomass had collapsed by May. The vertical distribution of chlorophyll across the Bank along Line 7 (Fig. 1) is shown in Fig. 5.

Survey mean nitrate concentrations, integrated to the bottom (Z_{max}), showed less monthly or interannual variation than for chlorophyll, but significantly (Kruskal-Wallace ANOVA; $p<0.05$) higher values were observed in March and April 1985 (Table 3). The area means, integrated to 50 m (not shown), indicate an offshore gradient, with the lowest concentrations consistently in Area 1 and the highest concentrations in Area 3. The shoaling of the nitracline over the deep water (Area 3) is coupled with doming upward of the isopycnals in this region and some geostrophic adjustment of the density field in the channel separating Browns Bank and the inshore region (e.g. see Smith 1989a; Fig. 9). Vertical nitrate distributions along Line 7 during April 1983, 1984, and 1985 (Fig. 6) illustrate the higher nitrate concentrations in 1985 compared with the previous two years, despite the much greater chlorophyll concentrations (e.g. Fig. 3).

Comparison of chlorophyll and nitrate concentrations provides a means to identify the phase of the phytoplankton bloom during each survey, particularly with regard to possible differences in the timing of bloom initiation. We defined the "prebloom" state to be when low chlorophyll occurred with high nutrients, an "early" bloom when high chlorophyll coincided with high nutrients, a "mid-bloom" when high chlorophyll corresponded with low nutrients, and the "end-bloom" when low chlorophyll corresponded with low nutrients. Using this scheme, the survey in March 1983 (Fig. 7a) occurred during a prebloom phase, while the survey in April 1983 (Fig. 7b) was conducted during a mid- to end-bloom phase. In 1984, the March survey (Fig. 7c) was conducted during the mid-bloom phase, while the bloom was ending by the April survey (Fig. 7d). In 1985 (Fig. 7e and f), the March survey occurred during the early-bloom phase and the April survey during the mid-bloom phase.

Zooplankton displacement volumes, excluding sets in which ctenophores made a significant contribution to the volume estimate, were significantly greater (*t*-test; $p<0.05$) in April and May than February and March in both 1983 and 1984 (Table 3). In 1985, however, displacement volumes remained low ($<15\ mL \cdot m^{-2}$) until May, when they were twice the volumes of 1983 and 1984 (Table 3). Spatial comparisons of displacement volumes, as survey means within each of the five areas, indicated that zooplankton biomass remained low ($<15\ mL \cdot m^{-2}$) in Area 1 from February to May in all three years. The changes in mean survey displacement volumes indicated in Table 3 are therefore due to increases in the offshore areas (2 to 5). Among these offshore areas, Area 3 generally had the highest mean displacement volumes, although it was significantly greater (ANOVA, or Kruskal-Wallace test when variances were not homogeneous; $p<0.05$) only during May 1983 and March 1984. This pattern is consistent with the onshore–offshore distribution of zooplankton displacement volumes determined for June and July 1981–85 by Koslow et al. (1989), and with zooplankton dry weights measured during May 1985 and 1986 by Frank (1988).

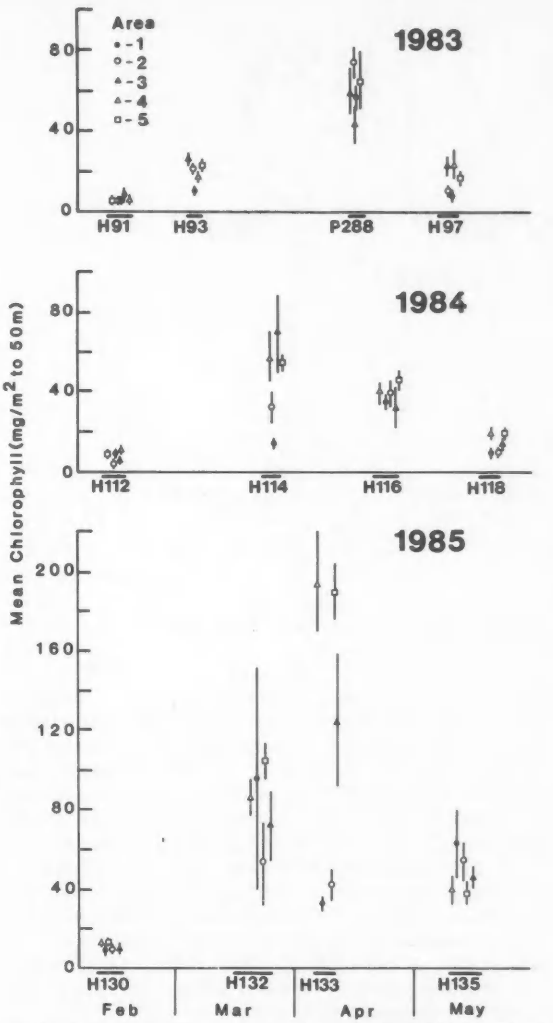


FIG. 4. Mean chlorophyll *a* concentrations (integrated to 50 m) for each survey and area, with area as defined in Fig. 2. Error bars represent ± 1 SE.

Monthly mean solar radiation for 1985 was significantly greater (Kruskal-Wallace ANOVA; $p<0.05$) during February, March, and April than corresponding months in 1983 and 1984 (Table 4). Mean surface wind stress, calculated from winds measured at Sable Island, decreased from February to May (Table 4) consistent with the reduction in pressure difference between the Icelandic low and the Azores high from winter to summer. Mean wind stress was similar between years, except for significantly (Kruskal-Wallace ANOVA; $p<0.05$) lower winds during April and May 1983.

Derived Parameters

The critical depth (Z_{cr}), the upper mixed-layer depth (Z_{mix}), and the potential energy anomaly to the critical depth ($\bar{\phi}_{Z_{cr}}$) were derived from the meteorological and physical oceanographic data. Survey means for these parameters are presented in Table 3.

Critical depths were smallest in February and largest in May, corresponding with the increase in solar radiation. They were of similar magnitudes during March and April, but with important interannual differences. Critical depths in March 1983 were significantly smaller (Kruskal-Wallace ANOVA; $p<0.05$) than in 1984 or 1985, corresponding to the lower solar radiation during 1983 (Table 4). The mean critical depth increased with each successive month in all years, except April 1985. This exception was due to greater attenuation of light through the water associated with the very high chlorophyll concentrations (and therefore high phytoplankton biomass) during that survey (e.g. Fig. 3).

Calculated mean mixed depths showed considerable variability both within and between years (Table 3). The general pattern was for mixed depths to decrease from winter to spring, which is consistent with the development of upper layer stratification due to surface warming and reduced wind stress. Spatially, the inshore and Browns Bank regions (Areas 1 and 5) had the shallowest mixed layers in February and March, since the bottom placed a lower limit to the extent of mixing. All areas had similar mean mixed depths in April, and by May the shallowest mixed layers occurred in the deep regions. This pattern represented the seasonal shoaling of the mixed layer, which occurred in all areas but was greatest in the deep water regions (e.g. Table 5).

The potential energy anomaly calculated to the critical depth ($\bar{\phi}_{Z_{cr}}$, Table 3) provides a measure of the stability of the water column. Values less than 5–10 $\mathrm{J \cdot m^{-3}}$ have been considered to represent well-mixed waters (e.g. Richardson et al. 1985). The only month that the mean potential energy anomaly exceeded 10 $\mathrm{J \cdot m^{-3}}$ was May, which corresponded with the mean mixed depths being smaller than mean critical depths.

The critical depth–mixed depth model requires critical depths to be greater than the mixed depth in order for net phytoplankton production throughout the water column to be positive. However, on the basis of the survey mean values presented in Table 3, this situation was not met until May, well past the spring bloom in all years. Since comparison of means may not represent the critical depth–mixed depth relationship at individual stations, these relationships were recalculated as the ratio Z_{cr}:Z_{mix} for each station, and summarized as medians by survey to reduce the influence of outliers (Table 3). Highest medians occurred in May in all years. However, during March and April, the year 1984 had higher median ratio values than 1985, whereas in fact the higher chlorophyll concentrations occurred in 1985. Note also that the spring bloom in all years occurred at median ratio values less than 1, i.e. with critical depths that were smaller than the depth of the mixed layer.

Model Results

Table 5 presents a comparison of mean mixed-layer depths observed during the surveys with mean modelled mixed-layer depths calculated for the same dates as each survey, separated into the five defined areas. In 50% of these areas, observed and modelled mixed depths agreed to within one standard error. The root mean squared deviation was 26 m, although if the variability of mixed depths within an area was considered so that the deviations were calculated from the closest standard error bar (and set equal to 0 if the standard errors overlapped), the root-mean-square deviation was 17 m. The only consistent pattern in the variation of observed and modelled survey-mean mixed depths between months and areas appeared to be a general trend for the model to overestimate mixed depths in winter and under-

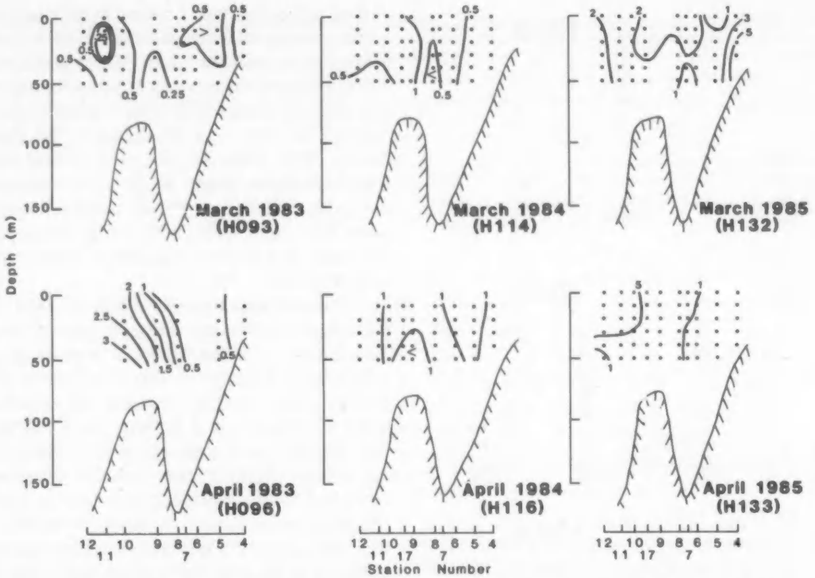


FIG. 5. Chlorophyll *a* concentrations (mg/m^3) along Line 7 (see Fig. 1) for surveys conducted in March and April 1983, 1984, and 1985. Survey H096 was conducted in this region from 21–27 April, 1983; it is included here because survey P288 sampled only a small part of Line 7.

estimate them in late spring. In comparing these results, it must be noted the survey-mean mixed layers were calculated from fixed stations sampled once during each survey (e.g. Fig. 1a), while for the modelled mixed depths, daily means over each area (e.g. Fig. 2) were calculated first and then averaged over the duration of the survey. The mean modelled mixed depths therefore include greater spatial and temporal resolution than the mean observed mixed depths.

To examine the extent to which variations in the daily mean modelled mixed-layer depths were reflected in observed changes in vertical stratification, modelled mixed depths for Area 2 were plotted (Fig. 8) against daily $\Delta\sigma_t$ (50–15 m) values from mooring C2, located on the 110-m isobath in Area 2. There was general agreement between periods of shoaling of the modelled mixed layer and increases in the vertical density contrast at C2. In particular, highest vertical density contrasts at C2 corresponded with shallowest modelled mixed layers which occurred after the beginning of April, and represent development of seasonal stratification. There was, however, a slight phase lag, with modelled mixed depths leading changes in the vertical salinity contrast by 5, 6, 5 d in 1983, 1984, 1985. The cross-correlations of the differenced time series, taking account of the phase lags, were 0.15 for 1983 and 1985 and 0.34 for 1984. This phase lag may represent the effect of spatial averaging over all of Area 2 for the model compared with a single location for C2 data. It may also imply that the vertical density structure responds more slowly to wind stress and surface heat fluxes than the 3-d steady state condition assumed by the model.

Area 1 had lower integrated mean light intensities during spring in each year, but slightly higher intensities during winter, due to the shallower depth and stronger tidal mixing (Fig. 9). The greatest range of light intensities occurred in Area 3, consistent with its greater depth and stronger stratification. Light intensities in Area 5 were intermediate between Area 1 and 3. Between years, there was considerable variability in the pattern of daily mean light intensities, especially with regard to peaks that exceeded the critical light intensity for net positive phytoplankton growth (19 $W \cdot m^{-2}$). In 1983, two large peaks occurred (in Areas 3 and 5) in mid-March, although mean light intensities above 19 $W \cdot m^{-2}$ were not sustained until after the beginning of April. In 1984, two peaks also occurred in late March, although of shorter duration than 1983, followed by a large peak in early April and relatively low intensities until May. Mean (modelled) light intensities in 1985 were highly variable, when several peaks exceeded the critical intensity in all three areas as early as mid-February. These periods of high and low light intensity represent transient mixing and stratification events that continued until mid-April.

Comparison of mean survey chlorophyll biomass from Fig. 3 with the time series of mean mixed-layer light intensities (Fig. 9) indicates that higher chlorophyll concentrations occurred with higher light intensities, and in particular with peaks in light intensities greater than 19 $W \cdot m^{-2}$. The relationship is also consistent between areas, where for example the low chlorophyll biomass in Area 1 during March 1984 (Cruise H114) corresponded to light intensities less than 19 $W \cdot m^{-2}$, while the higher chlorophyll biomass in Area 3 corresponded to intensities greater than 19 $W \cdot m^{-2}$. A correlation between survey mean chlorophyll biomass and mean mixed layer light intensities for the survey dates for all areas and years combined (excluding data for May) was significant ($p<0.05$) and accounted for 36% of the variation. However, the correlation was weakened by the high chlorophyll biomass observed in March 1985 (e.g. Fig. 3) which coincided with a period of low light intensities just 3 d after a large peak in light intensity (Fig. 9). If the 3-d time scale for phytoplankton growth (e.g. Savidge 1988) is considered and the high light intensities just preceding survey H132 included in the analysis, the amount of variation explained is improved to 42%.

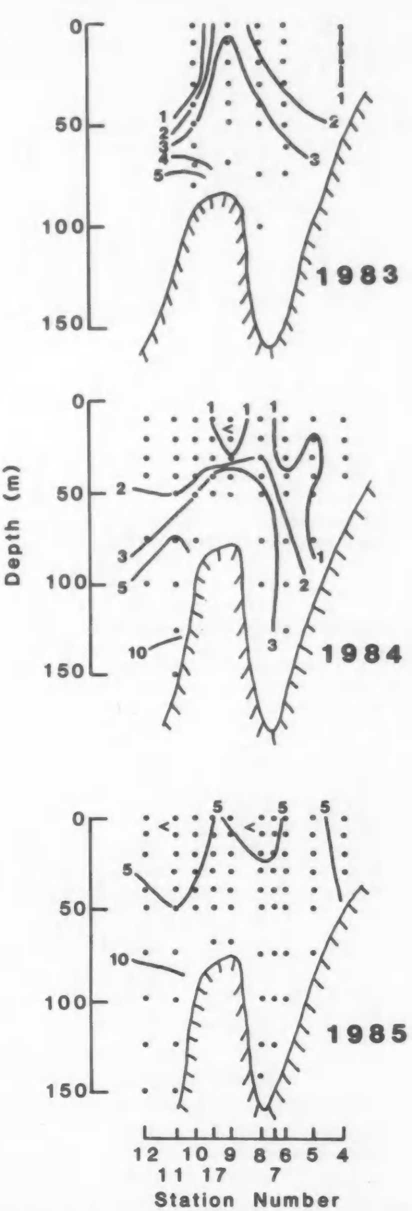


FIG. 6. Nitrate concentrations (μM) along Line 7 (see Fig. 1) for surveys conducted in April 1983 (H096), 1984 (H116), and 1985 (H133). Survey H096 was conducted in this region from 21–27 April, 1983; it is included here because survey P288 did not sample the entire Line 7.

Discussion

Observations of chlorophyll biomass from the Fisheries Ecology Program surveys off southwest Nova Scotia in 1983, 1984, and 1985 indicate the initiation of the spring phytoplankton bloom ranged from late March to mid-April. Densities of cod larvae show peak abundances in the region at this time, while densities of haddock larvae did not show marked increases until May or June (Campana et al. 1989).

Analysis of survey-mean chlorophyll concentrations (e.g. Fig. 3) suggests the bloom started earliest in 1984 and latest in 1983, but the highest biomass occurred in 1985. The chlorophyll–nitrate relationship for each survey also suggests the bloom was in progress during the survey in late March in 1984 (H114) and during the early April survey in 1985 (H133). The implication for 1983 is that the bloom occurred sometime in late March or early April. However, comparisons of the relative timing and magnitudes of the spring bloom between years is difficult due to the variable timing of the surveys. For example, it is not clear whether conditions sampled during the March 1984 survey represented the peak biomass of the bloom, or whether it continued to increase as occurred for the March and April 1985 surveys.

The Sverdrup critical depth–mixed depth concept is the model most often invoked to explain and predict the initiation of spring phytoplankton blooms. However, in this study the only month when survey-mean critical depth exceeded mean mixed depth was May, which was well past the observed timing of the bloom. May was also the only month when the potential energy anomaly calculated to the critical depth indicated stable conditions. The predictions of this model were not improved using medians of station-by-station critical depth–mixed depth ratios. The development of the spring bloom could not be explained by parameters measured during and calculated from the surveys, since they indicated blooms would have occurred in May. This finding does not invalidate the Sverdrup model, but implies instead that the spring bloom is initiated by processes occurring at times other than during the specific surveys, and that comparisons of interannual variability of bloom initiation cannot be made from surveys alone. We therefore chose to model the critical depth–mixed depth continuously through the late winter and spring, as a means to extrapolate between surveys and reduce the effect of variability in survey timing. Such a model also synthesizes the interannual variability of the important meteorological (wind and solar radiation) and oceanographic (advective fluxes of buoyancy) processes.

The results of the critical depth–mixed depth simulations agreed with observed increases in chlorophyll biomass. When surveys were conducted, higher observed biomass generally corresponded with mean light intensities through the modelled mixed layer that were greater than the critical value for a bloom to occur. The model also predicts spatial variability in light intensities consistent with the observed variability of chlorophyll biomass between areas (e.g. Fig. 4). Mean mixed-layer light intensities in Area 1 were usually lower than intensities in Areas 3 and 5, often failing to exceed the critical intensity, for example in mid-March 1983. This relationship between modelled light intensities and the chlorophyll biomass observed during the surveys was demonstrated by their significant correlation, and suggests the validity of the model for predicting phytoplankton blooms may be extended to periods when no surveys were conducted.

Therefore, the conclusions that can be derived from the model are that in the deep water areas in 1983, 1984, and 1985, the spring bloom was initiated in late March during brief periods of stability, with the principal bloom occurring in early April. In the more strongly-mixed shallow areas (e.g. Area 1), the bloom was delayed until early April. In 1985, the principal difference from the previous two years was the earlier and more frequent occurrence of periods of vertical stability sufficient to

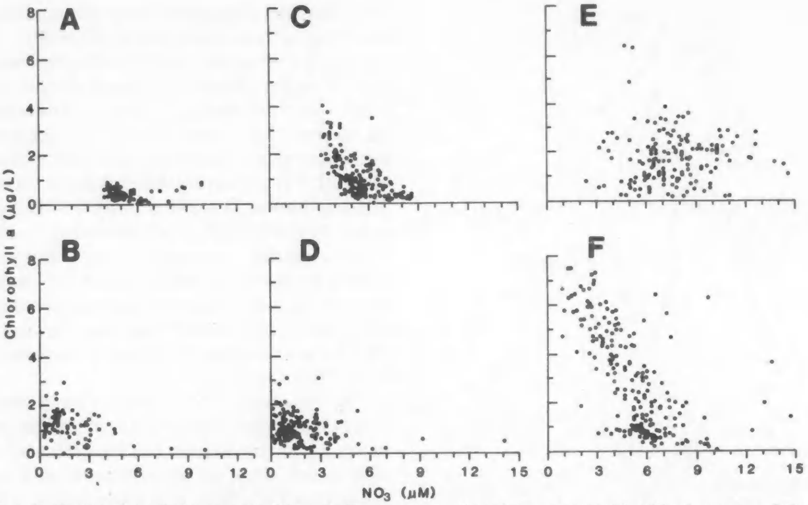


FIG. 7. Scatterplot of nitrate and chlorophyll *a* concentrations by survey to identify the stage of the spring bloom. (A) March 1983 (H093); (B) April 1983 (P288); (C) March 1984 (H114); (D) April 1984 (H116); (E) March 1985 (H132); (F) April 1985 (H133).

TABLE 5. Comparison of modelled mixed-layer depths with those measured on the surveys. Values are means (standard errors) in metres.

			Area				
Year	Cruise	Day of year	1	2	3	4	5
1983	H091	42-48	41(9)	64(20)	77(11)	64(17)	62(0)
	Model	42-48	50	76	82	78	72
	H093	63-65	38(6)	61(10)	87(21)	71(10)	41(7)
	Model	63-65	51	85	88	89	81
	P288	103-106	40(0)	55(20)	55(21)	44(13)	45(10)
	Model	103-106	37	50	64	56	46
	H097	126-130	32(8)	10(3)	52(16)	51(16)	43(6)
	Model	126-130	23	4	2	2	4
1984	H112	41-47	49(2)	41(23)	65(23)	71(16)	53(9)
	Model	41-47	50	69	73	67	62
	H114	81-86	30(15)	75(51)	66(20)	36(6)	79(60)
	Model	81-86	39	32	40	30	29
	H116	109-115	27(8)	43(10)	43(13)	69(8)	34(6)
	Model	109-115	37	27	24	24	27
	H118	136-141	35(5)	35(11)	32(17)	51(8)	38(6)
	Model	136-141	26	10	8	8	10
1985	H130	37-46	49(4)	35(15)	50(16)	38(8)	14(3)
	Model	37-46	48	66	87	70	62
	H132	73-83	—	73(19)	44(15)	49(16)	64(9)
	Model	73-83	48	79	110	93	74
	H133	93-98	50(5)	11(6)	51(8)	55(13)	31(7)
	Model	93-98	40	22	10	11	19
	H135	127-132	31(9)	54(13)	20(6)	37(10)	38(8)
	Model	127-132	37	33	30	32	31

produce mean light intensities greater than the critical value for rapid phytoplankton growth. Considering the short duration of such periods, net positive growth could not be sustained for more than a few days, but was sufficient to reduce the decline in the background biomass of phytoplankton.

The impact of such fluctuations on primary production can be assessed using the formula of Platt and Jassby (1976) for the relationship between photosynthesis and light intensity,

$$(9)\quad P^B = P^B_m \tanh\,(\alpha I/P^B_m) - R^B,$$

where P^B is the production per unit chlorophyll biomass (mg C (mg chl a)$^{-1}\cdot$ h^{-1}), P^B_m the assimilation number, I the light intensity (W $\cdot$ m^{-2}), R^B the respiration, and α the initial slope of the light saturation curve (mg C (mg chl a)$^{-1}\cdot$ h^{-1} $\cdot$ W$^{-1}\cdot$ m^2). Using mean values for α and P^B_m of 0.21 and 4.9, respectively (Platt and Jassby 1976), a value of 0.25 for R^B,

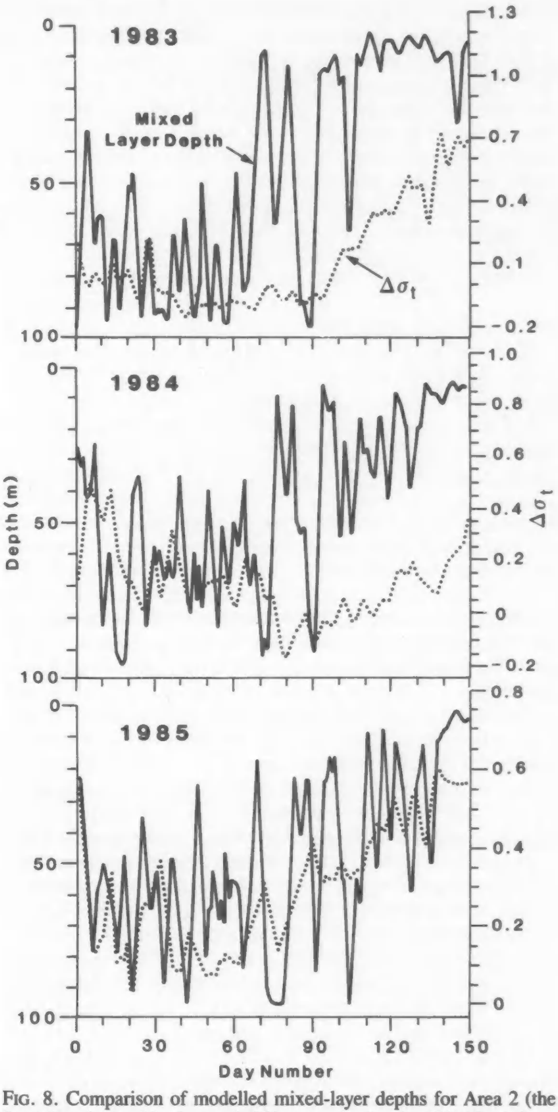


FIG. 8. Comparison of modelled mixed-layer depths for Area 2 (the frontal region) with observed differences in density (50–15 m) from mooring C2, located on the 110-m isobath in this area (see Fig. 1).

and I as the daily mean mixed-layer light intensity from the model for Area 3, the cumulative daily production (P^B) over spring for 1983–85 is presented in Fig. 10. It is assumed some fraction of this production would be converted into chlorophyll biomass. Figure 10 indicates greater production should have occurred in 1985, with a higher mean concentration in late winter than in previous years. This is consistent with the higher chlorophyll biomass observed on all surveys in 1985.

The influence of several factors may explain the observed high chlorophyll biomass in 1985. The alternation of mixing and stratification, combined with the higher monthly mean solar radiation in 1985, supported short increases in primary production which increased (or at least slowed the decrease of) phytoplankton biomass. Higher mean solar radiation acted both to reduce the mixed-layer depth, by increasing the surface heat flux, and to increase the mean mixed-layer light intensity for a constant mixed depth. Alternation of mixing and stratification also injects nutrients into the surface layer, ensuring sufficient substrate for phytoplankton growth during the next period of stratification. Clementson et al. (1989) noted that such periodic replenishment of nutrients supported an extended bloom of phytoplankton in waters off Tasmania. In addition to the effect of periodic stratification and mixing, nitrate concentrations in 1985 were higher throughout the study region, particularly in late spring. The water at 100 m at mooring C2 during spring 1985 was also generally the warmest and most saline of the study period. These conditions have been attributed to weak eastward components of the longshore wind stress in that year versus strong eastward components in 1983 and 1984 (Campana et al. 1989). Eastward wind stress drives an inflow of slope water into the Northeast Channel causing eastward heat and salt fluxes in the deep water at C2 (Smith 1989b). These relatively high salinities and nitrate concentrations at 50 m persisted into June 1985 (Koslow et al. 1989). Mean zooplankton biomass (measured as displacement volumes) remained low in 1985 until May. In particular, the low biomass during the April survey may also have enabled the large accumulation of phytoplankton biomass. Alternatively, the zooplankton biomass had not developed sufficiently by the time of the April 1985 survey to capitalize on the phytoplankton bloom. We are at present unable to distinguish between these two possibilities.

The spring phytoplankton bloom had collapsed in all years by the time of the surveys in May. This collapse was due to factors other than the mean mixed-layer light intensity, since this remained high in May with both a shallow upper mixed layer and high surface irradiance. One possible explanation is herbivore grazing, since zooplankton biomass was greatest in May of each year.

The conclusions of the model developed in this study imply that determining precisely when the spring phytoplankton bloom begins does not have a simple answer. In particular, it may occur as a single event in a specific region, for example at the end of March — beginning of April in 1984, or it may occur with a series of higher frequency stratification events which accumulate biomass gradually over spring, until such time as the seasonal pycnocline becomes firmly established, for example in 1985. Such brief stratification events would be very difficult to detect with ship-based observations, given fixed cruise schedules and the unpredictability of the appropriate mixing and solar radiation conditions. That such transient blooms do occur has been demonstrated by Lohrenz et al. (1988) for the Mediterranean, who also illustrated the utility of satellite observations for detecting these blooms. Thresher et al. (1989) also identified transient phytoplankton production pulses in the waters of Australia, and suggested they were responsible for pulses in the settlement of larvae of a temperate reef fish 7–9 wk later. They hypothesized the brief phytoplankton blooms provided food for newborn larvae, thereby enhancing their survival. In our study, no detailed data were available on the densities of zooplankton of the appropriate size for prey of larval fish (e.g. cod or haddock) on the same temporal scale as the phytoplankton bloom model. It is therefore not known whether such brief increases in primary production could lead to increases in zooplankton biomass, potentially increasing the supply of food to larval cod which appeared in the study region in mid-February (Campana et al. 1989). It is interesting to note that 1985 had the highest chlorophyll biomass in spring and the

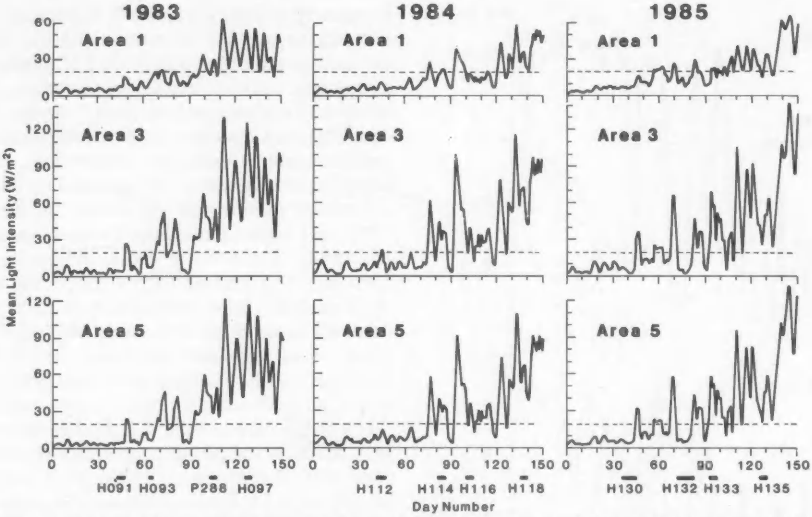


FIG. 9. Mean (modelled) mixed layer light intensities for Areas 1, 3, and 5 for 1983, 1984, and 1985. The dashed line indicates a value of 19 $w \cdot m^{-2}$, the critical value for the initiation of a phytoplankton bloom. The time of each survey is indicated along the bottom axis.

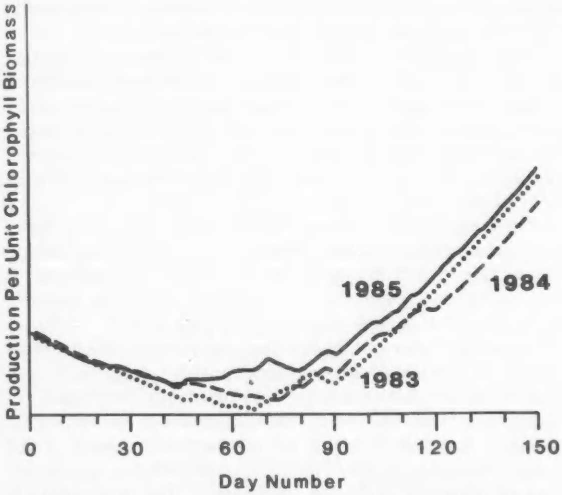


FIG. 10. Daily cumulative production per unit chlorophyll biomass calculated for an arbitrary starting concentration using the formula of Platt and Jassby (1976; see text). Input values are the mean modelled light intensity for Area 3 in 1983, 1984, and 1985 (i.e. Fig. 9).

highest abundance of cod larvae, although Campana et al. (1989) did not find subsequent larval survival was improved compared with 1983 and 1984.

The model developed here for the mixed-layer depth and the resulting mean light intensity contains several assumptions. The mixed depth is calculated on the basis of the balance between the dissipative processes of wind and tide against the buoyancy inputs of a surface heat flux and advection of salt (further assuming that the contributions of precipitation and evaporation are small relative to other terms). It does not take account of the different source regions of turbulent dissipation, other than to exclude tidal dissipation if the total depth is smaller than the bottom Ekman depth. Difficulties with choosing an appropriate formulation for reducing the contribution of tidal dissipation to the total turbulent dissipation near the surface have been presented by Loder and Greenberg (1986) and Bowers and Simpson (1987).

The contributions of differential horizontal advection of the density field to the buoyancy flux is also a difficult term to model. We have assumed that density is controlled mainly by salinity in this region, and that its vertical gradients are sufficiently linear to permit reduction of the density and horizontal velocity terms as described in Appendix I. Smoothing the daily vertical salinity contrast helps to reduce the high-frequency variability associated with baroclinic responses to atmospheric forcing, whose dominant time scales are in the range of 2 to 10 d (Smith 1989a). Another problem with modelling the differential horizontal advection term is the use of C2 measurements as a proxy for the horizontal buoyancy flux throughout the region. However, measurements at C10 on Browns Bank generally confirm the low-frequency pattern of variability at C2.

An important assumption is also made in calculating the average light intensity through the modelled mixed layer. Based on our data, we used two values for the attenuation coefficient for light through the water: 0.12 for days prior to Day Number 75 (16 March), and 0.13 for subsequent days. Actual attenuation coefficients are likely to be more variable, both temporally and spatially. However, it is believed these values are reasonable for modelling the initiation of the spring phytoplankton bloom off southwest Nova Scotia, based on the attenuation coefficients measured during the surveys. Advection into the region of phytoplankton from the Scotian Shelf or Gulf of Maine remains another potential source of chlorophyll biomass. However, since the meteorological conditions (and variability) are reasonably uniform over the entire southwest Nova Scotia area, the processes promoting blooms in the adjacent waters are likely to be similar to those described by this model.

Fournier et al. (1984b) suggested the planktonic environment off southwest Nova Scotia was influenced by five factors: seasonal stratification; tidal mixing; upwelling; the longshore residual circulation; and warm-core eddies (which are episodic and unpredictable). In summer, chlorophyll biomass distributions were dominated by inshore tidal mixing and offshore stratification, separated by a frontal region (Fournier et al. 1984b). However, in late fall phytoplankton biomass was influenced by the stratifying effects of high-salinity slope water offshore and low-salinity Scotian Shelf water near-shore (Fournier et al. 1984a). Koslow et al. (1989) show that advection of Shelf and Slope water masses, driven by large-scale atmospheric wind patterns, can also be important in structuring plankton distributions in early summer. Observations by Denman and Herman (1978) of Slope water in the southwest Nova Scotia region in late summer suggest such intrusions may be a common occurrence.

Therefore, control of plankton production processes off southwest Nova Scotia can be simplified to three factors: the amounts of light, nutrients, and herbivores, which are determined by the extent of vertical stratification and water mass exchange. The relative importance of these factors is seasonally variable, with light-limitation prevailing in winter, and nutrient limitation and grazing pressure in summer. Processes which increase stability, such as the intensity of solar radiation, surface winds, and the advection of Shelf or Slope water masses, are most important in fall, winter, and spring (Fournier et al. 1984a; this study). Processes which supply nutrients, for example advection of water masses and tidal mixing, are most important in summer (Fournier et al. 1984b; Koslow et al. 1989). Large-scale atmospheric pressure patterns and the resulting surface wind stresses play a major role in all seasons by influencing the vertical stability of the upper layer and the advection of Shelf and Slope water masses into the southwest Nova Scotia region.

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References

Bowers, D. G., and J. H. Simpson. 1987. Mean position of tidal fronts in European-shelf seas. Continental Shelf Res. 7: 35–44.

Bye, V. J. 1984. The role of environmental factors in the timing of reproductive cycles, p. 187–205. *In* G. W. Potts and R. J. Wootton [ed.] Fish reproduction. London, Academic Press.

Campana, S. E., K. T. Frank, P. C. F. Hurley, P. A. Koeller, F. H. Page and P. C. Smith. 1989. Survival and abundance of young cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue)

Clementson, L. A., G. P. Harris, F. B. Griffiths, and D. W. Rimmer. 1989. Seasonal and inter-annual variability in chemical and biological parameters in Storm Bay, Tasmania. I. Physics, chemistry and the biomass of components of the food chain. Aust. J. Mar. Freshwater Res. 40: 25–38.

Cushing, D. C. 1967. The grouping of herring populations. J. Mar. Biol. Ass. U.K. 47: 193–208.

Denman, K. L., and A. W. Herman. 1978. Space-time structure of a continental shelf ecosystem measured by a towed porpoising vehicle. J. Mar. Res. 36: 693–714.

Dorrestein, R. 1979. On the vertical buoyancy flux below the sea surface as induced by atmospheric factors. J. Phys. Oceanogr. 9: 229–231.

Fournier, R. O., R. Ernst, N. B. Hargreaves, M. Van Det, and D. Douglas. 1984a. Variability of chlorophyll *a* off southwestern Nova Scotia in late fall and its relationship to water column stability. Can. J. Fish. Aquat. Sci. 41: 1730–1738.

Fournier, R. O., M. Van Det, N. B. Hargreaves, J. S. Wilson, T. A. Clair, and R. Ernst. 1984b. Physical factors controlling summer distribution of chlorophyll *a* off southwestern Nova Scotia. Limnol. Oceanogr. 29: 517–526.

Frank, K. T. 1988. Independent distributions of fish larvae and their prey: natural paradox or sampling artifact? Can. J. Fish. Aquat. Sci. 45: 48–59.

Garrett, C. J. R., J. R. Keeley, and D. A. Greenberg. 1978. Tidal mixing versus thermal stratification in the Bay of Fundy and Gulf of Maine. Atmos. Ocean 16: 403–423.

Gieskes, W. W. C., and G. W. Kraay. 1975. The phytoplankton spring bloom in Dutch coastal waters of the North Sea. Netherlands J. Sea Res. 9: 166–196.

Greenberg, D. A. 1983. Modelling the mean barotropic circulation in the Bay of Fundy and Gulf of Maine. J. Phys. Oceanogr. 13: 886–904.

Hurley, P. C. F., and S. E. Campana. 1989. The distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in the waters off Southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Iles, T. D. 1964. The duration of maturation stages in herring. J. Cons. Int. Explor. Mer 29: 166–188.

James, I. D. 1977. A model of the annual cycle of temperature in a frontal region of the Celtic Sea. Estuarine and Coastal Mar. Sci. 5: 339–353.

Korn, G. A., and T. M. Korn. 1968. Mathematical handbook for scientists and engineers. McGraw-Hill, New York, 1130 p.

Koslow, J. A., R. I. Perry, P. C. F. Hurley, and R. O. Fournier. 1989. Structure and interannual variability of the plankton and its environment off Southwest Nova Scotia in late spring and early summer. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Loder, J. W., and D. A. Greenberg. 1986. Predicted positions of tidal fronts in the Gulf of Maine region. Continental Shelf Res. 6: 397–414.

Loder, J. W., C. K. Ross, and P. C. Smith. 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. Can. J. Fish. Aquat. Sci. 45: 1860–1885.

Lohrenz, S. E., R. A. Arnone, D. A. Wisenberg, and I. P. DePalma. 1988. Satellite detection of transient enhanced primary production in the western Mediterranean Sea. Nature (Lond.) 335: 245–247.

Niiler, P. P., and E. B. Kraus. 1977. One-dimensional models of the upper ocean, p. 143–172. *In* E. B. Kraus [ed.] Modelling and prediction of the upper layers of the ocean. Pergamon Press, Oxford.

Page, F. H., and K. T. Frank. 1989. Spawning time and egg stage duration in northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Banks. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

Parsons, T. R., Y. Maita, and C. M. Lalli. 1984a. A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford.

Parsons, T. R., M. Takahashi, and B. Hargrave. 1984b. Biological oceanographic processes. 3rd ed. Pergamon Press, Oxford.

Phillips, O. M. 1966. The dynamics of the upper ocean. Cambridge University Press, Cambridge.

Pingree, R. D., P. M. Holligan, G. T. Mardell, and R. N. Head. 1976. The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. J. Mar. Biol. Ass. U.K. 56: 845–873.

Platt, T., and A. D. Jassby. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol. 12: 421–430.

Pond, S., and G. L. Pickard. 1983. Introductory dynamical oceanography, 2nd ed. Pergamon Press, Oxford.

Richardson, K., M. F. Lavin-Peregrina, E. G. Mitchelson, and J. H. Simpson. 1985. Seasonal distribution of chlorophyll *a* in relation to physical structure in the western Irish Sea. Oceanologica Acta 8: 77–86.

Riley, G. A. 1957. Phytoplankton of the North Sargasso Sea, 1950–52. Limnol. Oceanogr. 2: 252–270.

Savidge, G. 1988. Influence of inter- and intra-daily light-field variability on photosynthesis of coastal phytoplankton. Mar. Biol. 100: 127–133.

Seber, G. A. F. 1973. The estimation of animal abundance and related parameters. Hafner Press, N.Y.

Simpson, J. H. 1981. The shelf-sea fronts: implications of their existence and behaviour. Phil. Trans. Royal Soc. Lond. A302: 531–546.

Simpson, J. H., and D. G. Bowers. 1984. The role of tidal stirring in controlling the seasonal heat cycle in shelf seas. Annales Geophysicae 2: 411–416.

Simpson, J. H., and J. R. Hunter. 1974. Fronts in the Irish Sea. Nature (Lond.) 250: 404–406.

SMITH, P. C. 1987. The distribution of surface wind over the Scotian Shelf, p. 25–36. Proceedings of the International Workshop on Wave Hindcasting and Forecasting, Halifax, N.S., September 23–26, 1986. Environmental Studies Revolving Funds, Report Series No. 65. Ottawa.

1989a. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

1989*b*. Seasonal and interannual variability off Southwest Nova Scotia. Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

SMITH, P. C., AND B. D. PETRIE. 1982. Low-frequency circulation at the edge of the Scotian Shelf. J. Phys. Oceanogr. 12: 28–46.

SVERDRUP, H. U. 1953. On conditions for the vernal blooming of phytoplankton. J. Cons. Int. Explor. Mer 18: 287–295.

TEMPLEMAN, W. 1972. Year-class success in some North Atlantic stocks of cod and haddock. ICNAF Spec. Publ. No. 8: 223–238.

THRESHER, R. E., G. P. HARRIS, J. S. GUNN, AND L. A. CLEMENTSON. 1989. Phytoplankton production pulses and episodic settlement of a temperate marine fish. Nature (Lond.) 341: 641–643.

TOWNSEND, D. W., AND R. W. SPINRAD. 1986. Early spring phytoplankton blooms in the Gulf of Maine. Continental Shelf Res. 6: 515–529.

VAN AKEN, H. M. 1986. The onset of seasonal stratification in shelfseas due to differential advection in the presence of a salinity gradient. Cont. Shelf Res. 5: 475–485.

WAIWOOD, K. G., AND M.-I. BUZETA. 1989. Reproductive biology of Southwest Scotian Shelf haddock (*Melanogrammus aeglefinus*). Can. J. Fish. Aquat. Sci. 46(Suppl.1): (This issue).

WRIGHT, D. G., D. A. GREENBERG, J. W. LODER, AND P. C. SMITH. 1986. The steady-state response of the Gulf of Maine and adjacent regions to surface wind stress. J. Phys. Oceanogr. 16: 947–966.

Appendix I

Calculation of Buoyancy Inputs due to Freshwater Fluxes

Buoyancy inputs to the waters off southwest Nova Scotia generally arise from two freshwater fluxes: (1) the excess of precipitation over evaporation at the surface, and (2) differential advection of the salt-stratified density field. Following Van Aken (1986), the general expression for the rate of change of potential energy in a water column of depth, h, is

$$\text{(A1.1)}\quad h\frac{d\bar{\phi}}{dt} = \frac{gh}{2}(\overline{w'\rho'})_0 + g\,\nabla_H\hat{\rho}\cdot\int_{-h}^{0}\tilde{\boldsymbol{u}}\,Z\,dZ - g \times \int_{-h}^{0}\overline{w'\rho'}\,dZ + g\,\hat{\boldsymbol{u}}\cdot\int_{-h}^{0}\nabla_H\tilde{\rho}\,Z\,dZ + g\int_{-h}^{0}\tilde{\boldsymbol{u}}\cdot\nabla_H\tilde{\rho} \times \left(Z+\frac{h}{2}\right)dZ + g\,\nabla_H\cdot\int_{-h}^{0}\overline{\rho'\boldsymbol{u}'}\left(Z+\frac{h}{2}\right)dZ,$$

where the overbar signifies a time average, ∇_H is a horizontal gradient, and the density (ρ) and horizontal velocity (u) have been decomposed into depth-average and vertically-varying means plus a turbulent component, i.e.

$$\boldsymbol{u}(x,y,z,t) = \hat{\boldsymbol{u}}(x,y) + \tilde{\boldsymbol{u}}(x,y,z) + \boldsymbol{u}'(x,y,z,t),$$
$$\rho(x,y,z,t) = \hat{\rho}(x,y) + \tilde{\rho}(x,y,z) + \rho'(x,y,z,t),$$

with $\int_{-h}^{0}\tilde{\boldsymbol{u}}\,dZ = \int_{-h}^{0}\tilde{\rho}\,dZ = 0.$

Neglecting horizontal divergences of the turbulent fluxes and using the turbulent kinetic energy equation to express the vertical integral of the buoyancy flux in terms of production and dissipation of turbulence gives,

$$\text{(A1.2)}\quad h\frac{d\bar{\phi}}{dt} = \frac{gh}{2}(\overline{w'\rho'})_0 - \epsilon_t' D_t - \epsilon_w\gamma D_w + g \times \int_{-h}^{0}(\tilde{\boldsymbol{u}}\cdot\nabla_H\hat{\rho} + \hat{\boldsymbol{u}}\cdot\nabla_H\tilde{\rho})\,Z\,dZ + g\int_{-h}^{0}\tilde{\boldsymbol{u}}\cdot\nabla_H\tilde{\rho} \times \left(Z+\frac{h}{2}\right)dZ.$$

Assuming weak vertical gradients, the mean density and velocity functions may be expanded about mid-depth in a Taylor series, i.e.

$$\text{(A1.3)}\quad \rho = \hat{\rho} + \tilde{\rho} \text{ « } \hat{\rho} + \rho_z\left(Z+\frac{h}{2}\right)$$
$$\boldsymbol{u} = \hat{\boldsymbol{u}} + \tilde{\boldsymbol{u}} \text{ « } \hat{\boldsymbol{u}} + \boldsymbol{u}_z\left(Z+\frac{h}{2}\right)$$

where ρ_z and $\mathbf{u}_z$ are the average stratification and vertical shear over the water column. Substituting into (A1.2) gives,

$$\text{(A1.4)}\quad h\frac{d\bar{\phi}}{dt} = \frac{gh}{2}(\overline{w'\rho'})_0 - \epsilon_t' D_t - \epsilon_w\gamma D_w + \frac{gh^3}{3} \times (\boldsymbol{u}_z\cdot\nabla_H\hat{\rho} + \hat{\boldsymbol{u}}\cdot\nabla_H\rho_z)$$

where the last term accounts for the buoyancy flux due to differential advection of the density field.

In order to relate the differential advection terms to measured quantities, return to the mass conservation equation,

$$\text{(A1.5)}\quad \frac{\partial\rho}{\partial t} + \nabla_H\cdot\rho\boldsymbol{u} = 0$$

where vertical advection and turbulent diffusion have been neglected. Assuming that density changes near the top (ρ_u) and bottom (ρ_L) of the water column are governed by horizontal advection in the y- (alongshore) direction results in

$$\text{(A1.6)}\quad \frac{\partial(\rho_u-\rho_L)}{\partial t} = \frac{\partial}{\partial y}(\rho_L v_L - \rho_u v_u)$$
$$= -\frac{\partial}{\partial y}(\hat{\rho}\,\Delta v + \bar{v}\,\Delta\rho)$$
$$= -\left(\Delta v\frac{\partial\hat{\rho}}{\partial y} + \bar{v}\frac{\partial\Delta\rho}{\partial y}\right)$$

where $\Delta\rho = \rho_u - \rho_L$, $\Delta v = v_u - v_L$, $\hat{\rho} = \frac{1}{2}(\rho_u + \rho_L)$ and $\hat{v} = \frac{1}{2}(v_u + v_L)$. (Notice that to lowest order, $\partial v/\partial y = 0$).

Applying these approximations to the differential advection terms in (A1.4) and assuming that density is controlled by salinity ($\rho = \rho_0\beta S$) gives

$$\text{(A1.7)}\quad \boldsymbol{u}_z\cdot\nabla_H\hat{\rho} + \hat{\boldsymbol{u}}\cdot\nabla_H\rho_z \text{ « } \frac{\Delta v}{\Delta Z}\frac{\partial\hat{\rho}}{\partial y} + \frac{\hat{v}}{\Delta Z}\frac{\partial\Delta\rho}{\partial y}$$
$$\text{« } -\frac{1}{\Delta Z}\frac{\partial(\rho_u-\rho_L)}{\partial t} = \frac{\rho_0\beta}{\Delta Z}\frac{\partial(S_L-S_u)}{\partial t}$$

where S_u and S_L are salinity measurements separated by the vertical distance, ΔZ.

Noting that the surface buoyancy flux including freshwater input is given by (Dorrestein 1979)

$$\text{(A1.8)}\quad B_0 = -\frac{g}{\rho_0}(\overline{w'\rho'})_0 = -\frac{g}{\rho_0}\left(\frac{\alpha Q}{c_p} + \beta S(P-E)\right)$$

where $P-E$ is precipitation minus evaporation, the potential energy equation reduces to

$$\text{(A1.9)}\quad h\frac{d\bar{\phi}}{dt} = -\frac{1}{2}\rho_0 h B_0 - \epsilon_t' D_t - \epsilon_w\gamma D_w + \frac{\rho_0 g h^3}{3\Delta Z}\beta\frac{\partial\Delta S}{\partial t}$$

where $\Delta S = S_L - S_u$ is measured vertically downward over a distance ΔZ.

Appendix II

Analytical Solution for the Mixed-Layer Depth Equation

This solution follows Cardan's method for cubic equations (Korn and Korn 1968). The governing equation

$$\text{(A2.1)}\ \frac{gh^3}{3\Delta Z}\rho_0\beta\frac{\partial\Delta S}{\partial t} + \frac{gh}{2}\left(\frac{\alpha Q}{c_p} + \rho_0\beta S(P-E)\right) - (\epsilon_t' D_t + \epsilon_w\gamma D_w) = 0,$$

may be rewritten in the form: (A2.2) $h^3 + ph + q = 0$, with

$$\text{(A2.3)}\quad p = \frac{3\,\Delta Z\,\alpha\,Q}{2\,\rho_0 c_p\beta}\left(\frac{\partial\Delta S}{\partial t}\right)^{-1} \text{ and}$$

$$q = -\frac{\epsilon_t' D_t + \epsilon_w\gamma D_w}{g\rho_0\beta\xi 3\Delta Z}\left(\frac{\partial\Delta S}{\partial t}\right)^{-1},\quad \frac{\partial\Delta S}{\partial t} \neq 0.$$

Using the positive roots, the solution is of the form

$$\text{(A2.4)}\quad h = A + B$$

where $A = \sqrt[3]{-q/2 + \sqrt{R}}$, $\qquad B = \sqrt[3]{-q/2 + \sqrt{R}}$
and $R = (p/3)^3 + (q/2)^2$.

The roots of the equation depend on the sign of R, and the layer thickness is maximum positive ($h = h_0$) when the daily increment in the vertical salinity contrast is $d\Delta S = d\Delta S_0$. This critical value is calculated from $R = 0$ and is given by,

$$\text{(A2.5)}\quad d\Delta S_0 = \frac{\partial\Delta S}{\partial t}dt = -\frac{\Delta Z\,dt}{2\,\rho_0\beta}\left(\frac{g}{3D}\right)^2\left(\frac{\alpha Q}{c_p}\right)^3$$

with $D = \epsilon_t' D_t + \epsilon_w\gamma D_w$. When the daily increment in vertical salinity contrast is less than $d\Delta S_0$, the only real solution to equation A2.1 is negative and therefore not physically reasonable. In this case, h is set to h_0. Thus, the solution of (A2.1) for h is derived by:

i) if $d\Delta S > d\Delta S_0$ and $R > 0$, use equation (A2.4)
ii) if $d\Delta S > d\Delta S_0$ and $R < 0$, use a trigonometric form of the solution which is continuous with that for case i) above (Korn and Korn 1968):

$$\text{(A2.6)}\quad h_1 = 2\sqrt{-\frac{p}{3}}\cos\left(\frac{\delta}{3} + \frac{\pi}{3}\right);\ \cos\delta = -\frac{q/2}{\sqrt{-(p/3)^3}}$$

iii) if $d\Delta S < d\Delta S_0$, set $h = h_0$
iv) if $d\Delta S = 0$, $h = -q/p$ from (A2.2).

Appendix III

Calculation of the Daily Heat Flux (Q) Through the Sea Surface (James (1977); Simpson and Bowers (1984))

The heat flux through the sea surface (Q) can be approximated by,

$$Q = Q_s + k(T_d - T_s),$$

with Q_s the solar flux at sea level, T_d the atmospheric dew point temperature, T_s the sea surface temperature (in the model calculations taken as the daily sea surface temperature at the 15-m level of mooring C2), and k a thermal exchange coefficient. The value of k is not constant, but depends on temperature and wind speed,

$$k = 4.5 + 0.05\,T_s + (\delta + 0.47)\,F(W)$$

where $\delta = 0.35 + 0.015\,T_m + 0.0012\,T_m^2$,

$$T_m = 0.5\,(T_s + T_d),$$

and the wind speed function $F(W)$ is

$$F(W) = 9.2 + 0.46\,W^2.$$

Note the units are Q (W·m^{-2}), k (W·m^{-2}·°C^{-1}), T (°C), and W (m·s^{-1}).

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Volume 46, Supplement No. 1, 1989 **Volume 46, Supplément nº 1, 1989**

Fisheries Ecology Program

Smith, P. C., K. T. Frank, and R. Mahon. General introduction to southwest Nova Scotia Fisheries Ecology Program (FEP): 1982–89 **2–3**

Smith, P. C. Seasonal and interannual variability of current, temperature and salinity off southwest Nova Scotia **4–20**

Page, F. H., and P. C. Smith. Particle drift in the surface layer off southwest Nova Scotia: description and evaluation of a model **21–43**

Koslow, J. A., R. I. Perry, P. C. F. Hurley, and R. O. Fournier. Structure and interannual variability of the plankton and its environment off southwest Nova Scotia in late spring and early summer **44–54**

Page, F. H., K. T. Frank, and K. R. Thompson. Stage dependent vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs in a stratified water column: observations and model **55–67**

Page, F. H., and K. T. Frank. Spawning time and egg stage duration in Northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank **68–81**

Frank, K. T., F. H. Page, and J. K. McRuer. Hydrographic effects on the vertical distribution of haddock (*Melanogrammus aeglefinus*) eggs and larvae on the southwestern Scotian Shelf **82–92**

Campana, S. E., S. J. Smith, and P. C. F. Hurley. A drift–retention dichotomy for larval haddock (*Melanogrammus aeglefinus*) spawned on Browns Bank **93–102**

Hurley, P. C. F., and S. E. Campana. Distribution and abundance of haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) eggs and larvae in the waters off southwest Nova Scotia **103–112**

Suthers, I. M., K. T. Frank, and S. E. Campana. Spatial comparison of recent growth in postlarval Atlantic cod (*Gadus morhua*) off southwestern Nova Scotia: inferior growth in a presumed nursery area **113–124**

Frank, K. T., and J. K. McRuer. Nutritional status of field-collected haddock (*Melanogrammus aeglefinus*) larvae from southwestern Nova Scotia: an assessment based on morphometric and vertical distribution data **125–133**

Mahon, R., and R. W. Smith. Demersal fish assemblages on the Scotian Shelf, Northwest Atlantic: spatial distribution and persistence **134–152**

Waiwood, K. G., and M.-I. Buzeta. Reproductive biology of southwest Scotian Shelf haddock (*Melanogrammus aeglefinus*) **153–170**

Campana, S. E., K. T. Frank, P. C. F. Hurley, P. A. Koeller, F. H. Page, and P. C. Smith. Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength **171–182**

Perry, R. I., P. C. F. Hurley, P. C. Smith, J. A. Koslow, and R. O. Fournier. Modelling the initiation of spring phytoplankton blooms: a synthesis of physical and biological interannnual variability off southwest Nova Scotia, 1983–85 **183–199**

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